NORTHERN CARDINAL RESPONSE TO BROOD PARASITISM BY BROWN-HEADED COWBIRDS

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ABSTRACT

NORTHERN CARDINAL RESPONSE TO BROOD PARASITISM BY BROWN-HEADED COWBIRDS

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The relationship between the brood parasitic Brown-headed Cowbird and a common host, the Northern Cardinal, was studied in 1993 and 1994 near Dayton, Ohio. The frequency and patterns of cowbird parasitism and cardinal responses to parasitism were determined. Nest site characteristics (nest height, nesting tree height, and nest cover) and host egg characteristics (size and shape) were compared between parasitized and nonparasitized nests to ask why particular hosts were parasitized. Cardinal plumage color (a possible age and/or "quality" indicator) was also compared between parasitized and nonparasitized birds.

Of the 122 nests studied, 46% were parasitized, and the mean number of cowbird eggs per parasitized nest was 1.3. Frequency (percentage of cardinal nests parasitized) and intensity (number of cowbird eggs laid per parasitized nest) of parasitism were found to be highest between late April and mid May, suggesting that cardinals may be a preferred host during this period due to the scarcity of other available hosts. Rejection behavior (i.e., nest abandonment or egg burial) was observed only three times, supporting the hypothesis that cardinals in this population are true "accepters" of cowbird parasitism. Nest success was higher in parasitized than nonparasitized nests as a result of higher

mortality of nonparasitized nests during egg laying. However, no difference in nest site characteristics between parasitized and nonparasitized nests was found, and no correlation between cardinal phenotype and frequency of being parasitized was found. Cardinals in this population may suffer only a moderate cost in being parasitized. The 0.43 egg per nest lost to cowbird removal is lower than estimates for other host species. Also, nestling cardinals in this population maintain growth and fledge from nests in the presence of one or even two cowbird nestlings. Consequently, selection on cardinals to evolve a defensive response to parasitism may be less than that on other host species and results in this population exhibiting little rejection behavior.

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INTRODUCTION

Brood parasitism has evolved in animals as a means for one individual to maximize its reproductive success while minimizing parental investment. Brood parasitism is a reproductive strategy that has been described as an individual of one species using the nest or the help of another species to raise its offspring (Emlen 1973, Rothstein 1990). This mode of reproduction has been observed in a few freshwater fish species, but is best known and most studied in insects and birds. In social insects, the parasite either kills the host queen or coexists with the host queen and uses host larvae to raise the parasitic young (Wilson 1971, Davies *et al.* 1989).

In birds, parasitic females lay their eggs in the nest of other species and use the host parents to incubate and raise the parasitic young (Payne 1977, Rothstein 1990). Hosts can incur large costs in being parasitized (sometimes reducing their reproductive success to 0% [Robinson 1992]) due to the parasites' reliance on its hosts for the care of its young, and the maximizing of the parasite's reproductive success. Thus, brood parasites may represent a substantial threat to the reproductive success of the host and represent a strong selective pressure for the evolution of host defenses against being parasitized. The parasite, in turn, adapts to these host defenses and evolves counter measures to avoid these defensive mechanisms. What results has been described as a coevolutionary arms race between the parasite and its host

(Davies *et al.* 1989, Rothstein 1990) and has produced various mechanisms of defense in host species (Rothstein 1976a,b), as well as elaborate means for maximizing the success of the parasite (Lack 1968).

In North America, much attention has been paid to the brood parasitic Brown-headed Cowbird (*Molothrus ater*) and its effects on host reproductive success. As an extreme host generalist, the cowbird is known to parasitize over 200 species (Friedmann 1971) and is thought to be one of the leading causes in North American songbird population decline (Brittingham and Temple 1983, Terborgh 1992). Thus, further investigation into the cowbird:host relationship is necessary to determine specific host responses to cowbird parasitism, document the possible current evolution of defensive mechanisms in particular host populations, and determine the detrimental effects of cowbird parasitism on host populations. Findings from such studies could well be useful in future conservation efforts.

In this investigation, the relationship between the Brown-headed Cowbird and a common host, the Northern Cardinal (*Cardinalis cardinalis*) was studied. Data were collected on the frequency and patterns of parasitism to determine its effect on cardinal reproductive success. In addition, the response of cardinals to parasitism was recorded through daily nest visits. Finally, mechanisms in female cowbird nest selection were examined.

LITERATURE REVIEW: THE BROWN-HEADED COWBIRD

The Brown-Headed Cowbird

General Characteristics

The Brown-headed Cowbird is a medium-sized passerine (family Icteridae), and is classified as a social obligate brood parasite, laying its eggs in the nests of other species. It is a sexually dimorphic species with the male being both more colorful and ca. 15 - 20% larger than the female (Baldwin and Kendeigh 1938, Weatherhead 1989). The difference in adult body size develops following fledging from the host nest (Weatherhead 1989). Adult males are clove brown over the head, throat, and nape, while the rest of the plumage is lustrous black with green and purple reflections. Adult females tend to be completely gray (Bent 1958). Immature cowbirds are dark olive brown on the sides of the head, neck, wings and tail, the feathers are edged with buff, the primaries are whitish, and the breast is streaked with olive brown (Bent 1958). Adult plumage is achieved prior to the first winter as the result of a postjuvenal molt that occurs in August and early September. This yearly molt occurs in adulthood as a postnuptial molt, again occurring in August and early September. Nuptial plumage is acquired the following spring as a result of feather tip loss due to wear.

The adult cowbird's diet consists of ca. 20% animal matter and 80% vegetable matter (Bent 1958). The animal matter consists mainly of insects and spiders, and the majority of the vegetable matter is from a variety of grains and

seeds (Bent 1958). Because nestlings are not fed by adult cowbirds, nestling diets will be dependent upon the typical foods brought to the host nestlings.

Annual survivorship of adults is between 50 and 60% (Arnold and Johnson 1983); however, the sex ratio of adults is commonly male biased. Although sex ratios for eggs and nestlings have been shown not to differ from unity (Weatherhead 1989), wintering roost populations are ca. 70% males (Arnold and Johnson 1983). The sex ratios from these same wintering populations ranged from 3:1 (males:females) to more than 8:1 (Arnold and Johnson 1983). Male biased sex ratios are also apparent on summer breeding grounds, generally ranging from 2-3:1 (Friedmann 1929, A. Ologhlen, pers. comm.). This apparent skew in adult sex ratios is considered to be a result of higher first year female mortality (Weatherhead 1989), but the cause of this higher mortality is not apparent.

Distribution and Habitat

Currently, the Brown-headed Cowbird is distributed throughout most of North America. It is believed that the cowbird was derived from South American ancestors and entered North America by expanding through Mexico (Friedmann 1929, Bent 1958). Prior to the 1800's it was primarily found in the open grasslands west of the Mississippi River where there was an abundance of potential hosts and feeding grounds (Mayfield 1965, Brittingham and Temple 1983). However, because of their dependence on open plots of short grass for feeding, cowbirds were unable to expand into the dense forests of the eastern United States. As human populations began to grow in North America and as forests were logged, cowbirds expanded their range. As eastern forests

diminished, cowbirds established populations in Pennsylvania and New York by 1790, and were noted as regular inhabitants of Ohio by the middle of the nineteenth century (Dawson 1903, Mayfield 1965).

With the increase in the range of the cowbird, there has also been an increase in cowbird density. As cowbirds have expanded their range, they have come into contact with new, naive hosts that have accepted cowbird parasitism (Mayfield 1965). Since these new hosts offered no resistance to this form of parasitism, cowbirds were able to increase their reproductive success. The expansion of southern agricultural land has also improved the area used by cowbirds as winter feeding grounds and increased the probability of an individual surviving to the next breeding season. Therefore, due to the abundance of hosts and an increase in suitable wintering habitat, cowbird numbers have increased dramatically. As a measure of this increase, Christmas bird counts of cowbirds in 11 southern states have increased from one bird in 1900 to 205 in 1980 (Brittingham and Temple 1983).

Evolution of Parasitic Behavior

The parasitic nature of the Brown-headed Cowbird is believed to have evolved as a result of its relationship with the roaming herds of bison (*Bison bison*) (Friedmann 1929, Hill 1976). Cowbirds were able to feed on insects that were flushed by herds of bison. However, because of the nomadic nature of bison, it became difficult for female cowbirds to incubate efficiently and care for their offspring while remaining with the herd. As a result, it is believed that they began to lay their eggs in the nests of other birds as they became available (Friedmann 1929). This adaptive behavior (Hamilton and Orians 1965) allowed

female cowbirds to reduce their parental investment, increase the number of eggs produced, and increase the period of time available for other behavior such as foraging and nest searching.

Although cowbird nestlings do not exhibit the elaborate adaptations of other brood parasites (e.g., cuckoos ejecting other eggs or young from the nest, or honeyguides using a mandibular hook to kill other nestlings present in the nest), cowbirds display characteristics intimately related to their brood parasitic nature. First, cowbirds have evolved a generalized pattern of parasitism. The Brown-headed Cowbird is known to parasitize over 200 different species (Friedmann 1971), in sharp contrast to the European Cuckoo (*Cuculus canorus*) which specializes on selected host species (Lack 1968, Rothstein 1990). Lanyon (1992) has shown that in the parasitic cowbirds, the generalized form of parasitism is the derived condition, while the specialist form is the more primitive. By becoming a generalized parasite, Brown-headed Cowbirds were able to avoid the defensive mechanisms employed by certain host species by using the nests of other naive species. In addition, as extreme generalists, cowbirds have probably decreased the pressure on potential hosts to evolve defensive behavior (Davies and Brooke 1989).

The Brown-headed Cowbird also has a generalized egg color pattern. Rather than mimicking eggs of a specific host species, cowbird eggs are similar to those of a variety of small songbird hosts. Cowbird eggs generally have a white to grayish white background, with specks and blotches varying in color from chocolate to cinnamon rufous (Bent 1958). This type of "general passerine egg" is also displayed by the ancestral, nonparasitic Bay-winged Cowbird (*Agelaioides badius*) (Lack 1968). The eggs of this species are described as

being a dirty white color, closely freckled or marbled with large and small spots of grayish brown (Friedmann 1929). Thus, Brown-headed Cowbirds may simply have maintained the ancestral egg appearance. However, evidence suggests that Brown-headed Cowbirds have evolved a thicker egg shell and a more rounded shape. These adaptations make it more difficult for host species to puncture and remove cowbird eggs (Spaw and Rohwer 1987, Picman 1989, Weatherhead 1991).

A final characteristic of the Brown-headed Cowbird that aids their reproductive success is a rapid rate of development. Cowbird eggs hatch after 10-12 days of incubation (Nice 1953, Bent 1958), generally sooner than eggs of potential hosts. This short incubation period is present in other non-parasitic Icterids including the Tricolored Red-wing (*Agelaius tricolor*) and Red-winged Blackbird (*Agelaius phoeniceus*), therefore, it is not an evolved adaptation for parasitism in cowbirds (Nice 1953). However, by hatching prior to the host eggs, the cowbird nestling receives food from the parental hosts prior to the hosts' offspring. This results in the cowbird nestling being significantly larger than host nestlings at the time of host eggs hatching. This initial difference in size results in the cowbird outcompeting host nestlings by monopolizing food presented to the nestlings.

Nest Discovery and Selection, and Egg Laying Behavior

Female cowbirds require nests of other species and spend much time searching for nests to parasitize (Lack 1968). One method of nest discovery is through the casual observation of host nest building activity (Payne 1973, Thompson and Gottfried 1976, 1981). However, host activity is not always

necessary for discovery. Female cowbirds have also been observed both walking across the forest floor silently searching for nests and flying a few feet above shrubbery, then abruptly landing in the vegetation with considerable wing flapping (Norman and Robertson 1975). This final behavior is a more aggressive search intended to flush incubating females, thus exposing nests to the parasite.

If a female cowbird discovers more than one nest, she probably actively selects one in which to lay an egg. Apparently, female cowbirds simply avoid laying in the open cup nests of some species (Hill 1976). Studies have also shown that the frequency of parasitism of known rejecter species is lower than that of known accepter species in the same geographic area (Scott 1977). Thus, female cowbirds may choose not to lay in some potential hosts nests and thereby avoid the defensive responses of that host. However, within accepter species, the characteristics used in nest choice are unclear.

Experimental and observational data suggest active nest choice by female cowbirds. A recent study has shown that female cowbirds have a larger hippocampus and probably better spatial memory than males, and may be able to remember information about nest sites (Sherry et al. 1993). Female cowbirds have been observed sitting briefly in newly completed cardinal nests (R. Breitwisch, pers. comm.) and peering into the nests of Ovenbirds (*Seiurus aurocapillus*) and Prairie Warblers (*Dendroica discolor*) without laying eggs in them (Hann 1941, Nolan 1978). Thus, female cowbirds may find nests and assess the suitability of these nests prior to laying eggs in them.

Host activity at the nest (i.e. nest building or egg laying) is thought to be one of the leading criteria for nest selection by female cowbirds, although

experimental observations have produced inconclusive results (Laskey 1950, Thompson and Gottfried 1976, 1981, Lowther 1979). Cowbird eggs have also been found laid in inactive nests left from previous nesting attempts (Freeman et al. 1990), abandoned nests (Hann 1941, Nolan 1978), and in nests following the onset of incubation (Norman and Robertson 1975), where -- even if they hatched -- nestlings would have almost no chance of successfully fledging. Other potential factors involved in female cowbird nest selection (e.g. nest and host egg variables) have been tested, but few have received support. King (1973, 1979) found that female cowbirds prefer to lay in nests containing two smaller host eggs, however, he found other variables such as nest location and structure to be unimportant in female cowbird nest selection. Nolan (1978) found no significant difference when he analyzed the heights of parasitized and nonparasitized nests, although he found a statistically insignificant trend for increased parasitism as nest height increased. Thus, the factors affecting female cowbird nest selection are still unclear. Further investigation is necessary to determine the role of nest location, size, and structure, as well as the possible relevance of host egg shape, volume, and color pattern, in female cowbird nest selection.

Cowbird egg laying begins in late April and continues through the middle of July (but varies depending on geographic location) (Bent 1958, Hill 1976, Payne 1976). Results from recent studies (Scott and Ankney 1980, 1983, Holford and Roby 1993) support earlier conclusions (Mayfield 1960, Scott 1963) that female cowbirds are capable of maintaining maximum reproductive activity for extended periods during the breeding season. Other studies have suggested that female cowbirds lay eggs in clutches usually consisting of ca. four eggs

(Norris 1947, Payne 1973, 1976). Following the completion of these clutches, females refrain from laying eggs for several days before starting a new clutch (Bent 1958, Payne 1973). Reports on the number of eggs laid by an individual female in a breeding season vary, but average ca. 25 (Bent 1958), although Scott and Ankney (1980 and 1983) report that an average cowbird female lays about 40 eggs, and Holford and Roby (1993) report an individual captive female laying 77 eggs in a single breeding season.

Female cowbirds are known to lay their eggs in near darkness in the hour prior to sunrise. Observations on acts of parasitism describe females silently flying directly to the host nest and spending only about a minute inside the nest (Hann 1941, Neudorf and Sealy 1994). The short period spent at the nest and the lack of vocalizations during an act of parasitism suggest that inconspicuous behavior by female cowbirds is an adaptation decreasing the probability of detection by the host. Direct flight to the nest suggests that cowbirds remember nest site characteristics and know the area surrounding the nest prior to parasitizing the nest. Thus cowbirds have evolved means to minimize the risk of detection and maximize the probability of success.

In summary, Brown-headed Cowbirds display a suite of adaptations related to their highly specialized reproductive behavior. They represent what is potentially a formidable selective force on host species, dramatically decreasing host success, while simultaneously engaging in a coevolutionary arms race with these same hosts.

NORTHERN CARDINAL RESPONSE TO BROOD PARASITISM BY BROWN-HEADED COWBIRDS

INTRODUCTION

Brown-headed Cowbird (*Molothrus ater*) brood parasitism is a well known and well studied phenomenon. Much work has been done analyzing the costs paid by hosts in being parasitized through the removal of eggs by female cowbirds and as a result of cowbird nestlings outcompeting host nestlings for food. These costs have a significant effect on the reproductive success of some hosts, in some cases reducing it to 0% (May and Robinson 1985, Robinson 1992), and cowbird parasitism is considered one of the leading causes in the decline of Northern American songbird populations (Terborgh 1989, 1992).

Since cowbird parasitism represents a substantial threat to the reproductive success of the host species, it also represents a strong selective pressure for the evolution of host defenses against it. Four defensive mechanisms against cowbird parasitism have been documented in host species: 1) actively defending nests, 2) abandoning parasitized nests, 3) building a second layer over the already existing nest, thereby burying the eggs already present in the nest, and 4) ejecting cowbird eggs (Rothstein 1990). Continued investigation into specific host:cowbird relationships is necessary to determine general patterns in the evolution of host defenses and to analyze the costs to particular hosts in being parasitized.

Another subject of study is cowbird nest choice. Though nest searching behavior has been described (Norman and Robertson 1975), little is known

about how female cowbirds find nests to parasitize, and less is known about how they choose which nests to parasitize (King 1973, Thompson and Gottfried 1976, 1981). It is thought that host activity at the nest (i.e., nest building or egg laying) is one of the leading criteria for nest discovery and choice. However, observational and experimental evidence is insufficient to determine the role of host activity at the nest in nest discovery and selection (Laskey 1950, Thompson and Gottfried 1976, 1981).

Recent findings suggest that nest choice may not be entirely random. It has been shown that female cowbirds have a larger hippocampus than males, thus females probably have better spatial memory than males, and may be able to assess information about nest sites (Sherry *et al.* 1993). Female cowbirds have been seen sitting briefly in newly-completed nests (R. Breitwisch, pers. comm.), and peering into nests without laying eggs in them (Hann 1941, Nolan 1978). Since it is thought that female cowbirds are capable of finding several nests in a given day, these recent findings suggest that female cowbirds may actively choose which nest to parasitize. Though the criterion used by female cowbirds in assessing the suitability of nests are unknown, it has been suggested that cowbird nest choice may be based on characteristics such as nest placement, nest size, and/or nest contents (Thompson and Gottfried 1981).

In the current study, the relationship between the Brown-headed Cowbird and the Northern Cardinal (*Cardinalis cardinalis*) was analyzed. The cardinal is an appropriate subject species because it has been considered an accepter species of parasitism (Friedmann 1929, 1963, Rothstein 1975a,b) and is known to suffer high rates of parasitism (Hill 1976). However, cardinals are also known to abandon or bury eggs occasionally in response to cowbird parasitism (Bent

1968, Hill 1976, Graham 1988), and though no visual evidence of egg ejection has been noted (Rothstein 1971), rates of cowbird egg removal in parasitized cardinal nests suggest possible egg ejection (Scott 1977). Adults are also known to respond to a female cowbird model placed near the nest, though responses varied considerably, from little or none to highly aggressive defense (Nealen 1993). This intrapopulational variation suggests that differences exist in the behavior of cardinals and may be related to age and/or experience with being parasitized.

In addition, cardinal plumage differences may covary with incidence of parasitism. If plumage is an age indicator (S.A. Halkin, pers. comm.), brighter plumage may reflect an individual's level of experience with cowbirds and predict more aggressive defense. Alternatively, cardinals with the brightest plumage may be the best providers of food to nestlings (cf Hill 1991, R. Breitwisch, pers. comm.). Cowbirds could then use variation in plumage coloration to determine which nests to parasitize, choosing individuals who will be predictably better caregivers.

In this study, the reproductive success of individual cardinals and the frequency of cowbird parasitism was monitored. Patterns of parasitism were also analyzed to determine the costs paid by cardinals in being parasitized and their response to parasitism. Last, nest site variables and egg size and shape were analyzed to determine if they differed between parasitized and nonparasitized nests. Differences among clutches of cardinal eggs may be a cue used by female cowbirds in nest choice if female cardinals reject foreign eggs in proportion to their relative difference from the cardinals' own eggs. Female cowbirds may also use nest site characteristics as a cue to determine

which nests to parasitize if differences in nest sites correlate with nest success.

MATERIALS AND METHODS

Study Site

This study was conducted on the Aullwood Audubon Center and Farm property (39° 52' N and 84° 16' W), approximately 15 km NW of Dayton, Ohio from April to August 1993 and 1994. The property consists of approximately 80 ha, and although it is primarily reclaimed farmland, a variety of habitats are present (for a more detailed description, see Filliater *et al.* 1994). Approximately 30 to 40 pairs of Northern Cardinals reside year-round on the property (R. Breitwisch, T. Filliater, and P. Nealen, unpublished data). Cowbirds are common in all habitats on the property and are known to have occurred on the property since 1957 (J. Ritzenthaler, pers. comm.). Most of the observations in 1993 and all observations in 1994 were conducted in the southern half of the Aullwood property where ca. 25 adult pairs of cardinals on adjacent territories were studied.

Bird Capture

It was necessary that cardinals be individually identifiable in order to investigate responses to parasitism by different individuals and to monitor the success of any given individual throughout the breeding season. Cardinals were mist-netted during the breeding season, both at seasonal feeders and on their territories. Sixteen adults were captured in 1993, and an additional 15 adults

banded in previous years were present on the study area. In 1994, 38 adults were captured, and 22 adults from previous years were present on the study area. At capture, birds were marked with a USFWS numbered aluminum band and three colored celluloid bands. Plumage characteristics were recorded using the Munsell Color system (see Filliater-Lee 1992). Two regions on each bird (breast and bill for males, underwing and bill for females) were scored according to the value, hue, and chroma of the most closely matching color chip in the Munsell system. Whenever possible, two observers agreed on the most appropriate chip in order to maximize accuracy.

Nest Location and Observation

Nests were located both by actively searching appropriate habitats and by using behavioral cues of parental birds attending active nests. Whenever a nest was found, its location and stage of activity were recorded. During 1993, a total of 73 active nests were found (42 were being built, seven were receiving eggs from a female, 22 had eggs that were being incubated, and two had nestlings). Data were collected from 55 of the 73 nests (eggs were never found in 10 nests that were built, one nest was too high to study, and predation occurred in seven nests prior to data being taken on eggs or nestlings). In 1994, 78 active nests were found (35 being built, eight receiving eggs, 27 with eggs being incubated, and eight with nestlings present). Data were collected from 67 of these nests (predation occurred in five nests prior to data being collected, and data at six nests were not taken due to nest location). Nest progress was monitored until either young fledged or were preyed upon. Following three days of no activity at the nest after the contents of the nest disappeared, it was concluded that the

nest had been abandoned.

Active nests were visited usually every other day to monitor the progression of the breeding attempt. During the egg laying period, nests were visited daily until the onset of incubation. At each nest visit, the contents of the nest were observed using either a handheld mirror or a mirror on the end of a pole. Newly discovered eggs were uniquely marked on the more pointed end with black, indelible ink, and measurements for length and maximum breadth (to the nearest 0.1 mm) were taken using dial calipers. Eggs were marked to monitor egg laying sequence and possible changes in nest contents between visits. During nest visits, I waited until I was sure that no cardinals were near the nest before approaching the nest to handle eggs. The average nest visit lasted ca. two minutes. Rarely during the egg laying stage did a cardinal return to the nest while I was present, and none of these abandoned the nesting attempt.

At the onset of incubation, nests were visited every other day to monitor activity. Whenever possible, the nest was observed through binoculars from a distance of greater than five meters to avoid disturbance. If the parent birds were not present, nest contents were viewed using a mirror. On day six or seven of incubation, eggs were removed to determine if marked eggs had disappeared. If new unmarked eggs were found in the nest they were marked and measured, and all eggs present in the nest were photographed. During visits, I waited until the female left the nest before approaching to handle eggs. Despite these precautions, approximately 25% of trips were terminated or hurried because an adult returned to the nest; however, there was no case of abandonment apparently due to my presence at the nest.

Similar procedures were followed after the eggs had hatched. Nests were visited every other day to monitor activity, and six days after hatching, nestlings were carefully counted and species identified. In 1994, to determine if the development of cardinal nestlings differed in parasitized and nonparasitized nests, a sample of cardinal nestlings were weighed on about the sixth day of brooding using a standard spring balance. Nestlings were also banded at this time for future identification. Young were not presumed to have fledged unless they were seen or heard on the breeding territory at the appropriate age for fledging (ca. 9 -11 days after hatching).

Nestling cardinals and cowbirds less than 3-4 days old are quite similar in appearance, and only infrequently was it possible to determine species identity of young nestlings. As nestlings aged, differences between cardinals and cowbirds become more apparent, due to the development of crest feathers and differences in bill flange coloration, and species determination was possible at about six days of age.

Nest success or failure was recorded for all nests. Nests were discovered at various stages in the nesting cycle, and many were already at the complete clutch or nestling stage. This bias in time of discovery can lead to an estimate of nest success for the population higher than the true nesting success (Mayfield 1961, 1975). Therefore, success per nest-day observed was calculated for the three stages of the nesting cycle (nest-building and egg-laying, egg incubation, and nestling) and compared between parasitized and nonparasitized nests. A per day mortality rate for each of the three stages was calculated by dividing the number of nests lost by the total number of nest-days observed in each stage. The mortality rate for the entire period was then calculated by multiplying the

mortality rate per day for the period by the length of the period. The success rate for each period was then calculated as $(1-r)^d$, where r equals the mortality rate per day and d equals the period in days of each stage. Based on prior observations, and using the methods of Filliater *et al.* (1994), five days was used as the period from the end of nest building through egg laying, 12 days was used for the egg incubation period, and 10 days was used for the nestling period. To calculate the overall success rate from nest-building to fledging, the success rates for each of the three stages were multiplied together.

Egg Color, Size and Shape

Cardinal and cowbird eggs are similar in background color and color and pattern of spotting. The background color of cardinal eggs is grayish white. They are well speckled and spotted with different shades of brown. The markings are fairly evenly distributed with a tendency to become more concentrated towards the large end (Bent 1968). The background color of cowbird eggs varies from almost pure white to grayish white, and the entire surface is usually covered with specks and blotches of varying shades of brown (Bent 1958).

Egg size and shape were measured to determine the species of each egg and to what degree cardinal and cowbird eggs differed. Egg measurements (to the nearest 0.1 mm) for length (L), and maximum breadth (B) were taken using dial calipers. Length and breadth measurements were compared with literature values for cardinal and cowbird eggs to determine species (data in Bent 1958, 1968). From these measurements, egg volume was calculated using the standard formula for an ellipsoid ($V = \pi LB^2 / 6$) (Worth 1940). The value for egg

elongation was also calculated using the ratio of length : maximum breadth (Preston 1968, 1969, 1974).

For statistical analyses, each cowbird egg found was taken as an independent datum because it is thought that female cowbirds rarely lay more than one egg into any given nest (Bent 1958). Cardinal eggs were separated into two groups, those found in parasitized nests and those found in nonparasitized nests to determine if there was a difference in egg size and shape between the two groups. Differences between these two groups might suggest a basis for cowbird nest selection and/or cardinal egg recognition.

Nest Site Variables

Nest site variables were measured to determine if nest location differed between parasitized and nonparasitized cardinal nests. Tree height, height of nest, and nest coverage were measured following methods of Filliater et al. (1994). These data were collected near the end of July 1993 and throughout the 1994 breeding season. Data were collected following the completion of any nesting attempt. In 1993, nests with site characteristics changed by seasonal vegetation growth or the act of disruptive predation were not included. The height of the nest above ground, and the height of the nesting tree were measured to the nearest 0.1 m using a standard tape measure. Nest height measurements were taken from the rim of the nest to the ground. If tree height or nest height could not be measured accurately, measurements were taken to the highest point, and then estimated to the nearest meter using the prior measurement as a reference point. Nest coverage data were collected at the same time as the height measurements. Visibility (yes = 1 or no = 0) was

recorded from the four major directions (N, E, S, W) at nest height. Data were also collected from ground level below the nest, and from a meter above the nest. The overall coverage score for each nest was calculated by summing the visibility scores from all six directions. To avoid any bias, the assistant collecting the nest data was "blind" to nest status (parasitized vs. nonparasitized).

Statistical Analysis

Due to small to moderate sample sizes and unknown underlying distributions of data, nonparametric analyses were used in analyzing the results of this study. As non-parametric tests require no assumptions of distributional normality, their use is appropriate (Siegel 1956, Siegel and Castellan 1988).

Mann-Whitney U-tests (test statistic: U) were used to test for differences between two population means, such as comparisons between cardinal egg volume in parasitized and nonparasitized nests. Kruskal-Wallis One-Way ANOVAs (test statistic: H) were used to test for differences among three population means, such as comparisons among egg elongation of cardinal eggs (those found in parasitized and nonparasitized nests) and cowbird eggs. Friedman's method for randomized blocks (test statistic: X_r^2) was used to test for a sequence effect in the size and shape of cardinal eggs laid by an individual female. The Kolmogorov-Smirnov Two-Sample Test (test statistic: D) was used to test for differences in the distribution of two samples of continuous observations such as the number of cardinal nests parasitized per five day period. Spearman's Coefficient of Rank Correlation (test statistic: r_s) was used to determine the strength of correlations between variables such as cardinal plumage and the frequency of being parasitized. G-tests (test statistic: G) were

used for tests of association. Wilcoxon's Signed-Ranks Test for Two Groups (test statistic: T_s) was used to test for differences between two matched observations such as an individual cardinal's frequency of parasitism between 1993 and 1994 (Sokal and Rohlf 1981). All tests were two-tailed unless otherwise stated. All analyses were corrected for small sample sizes, if necessary. The α value for significance of statistical tests was set at $p=0.05$.

Similar descriptive data were collected in 1993 and 1994. Yearly data were compared, and if no difference was found, the data were combined in order to increase sample size.

RESULTS

General Patterns of Parasitism

Nesting data were collected from 122 cardinal nests during the two years of study (55 in 1993 and 67 in 1994). These nests were found at all stages of the nesting cycle (nest building, egg laying, and nestling stages). Parasitism occurred in 46% (56/122) of these nests (25 of 55 nests in 1993, 31 of 67 in 1994). Fourteen (25%) of these parasitized nests were multiply parasitized (11 nests with two cowbird eggs, and three nests with three cowbird eggs). The mean number of cowbird eggs laid per parasitized nest was 1.30 ± 0.57 (n=56). These values are conservative if cowbird eggs were removed prior to nest discovery or between daily nest visits.

The time of parasitism within the nesting cycle was determined for 30 nests (15 in 1993, 15 in 1994). The majority of nests (83% [25/30]), were parasitized during the egg laying period, with ca. 50% of the parasitic events occurring on day two of cardinal egg laying (day 1= day of the first cardinal egg). In two nests, a cowbird egg was found prior to the first cardinal egg, and once parasitism occurred following the onset of incubation. In the remaining two nests, multiple acts of parasitism occurred at different stages. The first nest was parasitized prior to the first cardinal egg and on day one of egg laying, while in the final nest parasitism occurred on the final day of egg laying and after incubation had begun. Three times during the study cowbird eggs were found in nests thought to be predated (eggs or nestlings were found in the nest, and the

next day only a single cowbird egg was present in the nest). These nests were not considered parasitized because it was thought that the act of parasitism occurred following the termination of a nesting attempt, and the female cardinal attending these nests had apparently abandoned the nest following predation.

To determine the seasonal patterns of cardinal and cowbird egg laying activity, the breeding season was divided into five day intervals (as in Hill 1976), and the dates of clutch initiation and any act of parasitism were noted for 106 nests. When nests were discovered after parasitism had occurred, they were back dated (using 12 days for the incubation period, and ten days for the nestling period) to determine when clutches were laid. This method for determining seasonal pattern assumes equal effort by the observer throughout the season.

Cardinals and cowbirds in southwestern Ohio began breeding in mid-late April. No yearly difference was found in the frequency distribution for the initiation of cardinal clutches ($D=0.24$, $n_1=46$, $n_2=60$, $p>0.10$) (Fig. 1). No yearly difference was found in the frequency distribution of cowbird eggs laid in cardinal nests ($D=0.15$, $n_1=30$, $n_2=39$, $p>0.5$) (Fig. 2). There was also no difference in the frequency distributions of cardinal clutches and cowbird eggs ($D=0.97$, $n_1=106$, $n_2=69$, $p>0.9$).

The temporal frequency distribution of the number of parasitized nests did not differ between years ($D=0.13$, $n_1=22$, $n_2=31$, $p>0.05$), thus the data from 1993 and 1994 were pooled. Parasitism was recorded to occur from 24 April to 15 July, with the highest number of parasitized nests being found between 26 April and 20 May (Fig. 3). When data were pooled into nine 10-day intervals, there was a significant negative correlation between the frequency of parasitism

and the period within the breeding season (r_s= -0.77, n=9, 0.05>p>0.02). Thus, the frequency of parasitism in cardinal nests decreased as the season progressed.

Patterns of parasitism within the breeding season were also measured by the intensity of cowbird parasitism (the number of cowbird eggs found per nest within a five day period). Within the breeding season, the intensity of parasitism varied from 0 - 2.25 cowbird eggs per parasitized nest, with the highest intensity occurring between 26 April and 30 April (Fig. 4). However, when data were pooled into nine 10-day intervals, there was no correlation between the intensity of parasitism and the period within the breeding season (r_s= -0.05, n=9, p>0.5).

Egg and Nestling Success

The percentage of cardinal eggs producing fledglings was analyzed to determine both the overall reproductive success and the effects of cowbird parasitism on this population of cardinals. Overall, 26% (n=239) of the cardinal eggs and nestlings that were found, fledged successfully. There was no yearly difference in the percentage of young fledged (23/107 in 1993, 39/132 in 1994) (G_{adj}=1.99, df=1, 0.5>p>0.1). There was also no difference in the percentage of young fledged from eggs in parasitized and nonparasitized nests (33/116 in parasitized, 29/123 in nonparasitized) (G_{adj}=0.72, df=1, 0.5>p>0.1), although the percentage of eggs producing fledglings was higher in parasitized nests.

To determine the frequency of female cowbird removal of cardinal eggs, egg disappearance was noted, and differences in the number of cardinal eggs laid and the number of cardinal eggs present at the onset of incubation were determined. Similarly, since female cowbirds are known to remove host eggs

during incubation (Scott *et al.* 1992), the number of cardinal eggs lost from laying to hatching in parasitized and nonparasitized nests was compared. The number of cardinal eggs laid did not differ between parasitized and nonparasitized nests ($U=218.5$, $n_1=23$, $n_2=17$, $0.4>p>0.2$), nor did the number of cardinal eggs present at the start of incubation ($U=247$, $n_1=23$, $n_2=17$, $0.2>p>0.1$) (Table 1).

In 23 parasitized and 17 nonparasitized nests the sequence of egg laying was known and incidents of egg removal were analyzed. A total of 14 cardinal eggs were removed from 10 of 23 parasitized nests, while three cardinal eggs were removed from two of 17 nonparasitized nests. Thus, a mean of 0.61 eggs were removed from parasitized nests, and 0.18 eggs from nonparasitized nests. Numbers of cardinal eggs removed from parasitized and nonparasitized nests during the egg laying stage were different ($U=256.5$, $n_1=23$, $n_2=17$, $0.05>p>0.02$). A difference was also found in the number of parasitized and nonparasitized nests which had an egg removed during egg laying ($G_{adj}=4.82$, $df=1$, $0.05>p>0.025$). There was no difference in the number of cardinal eggs lost from incubation to hatching in parasitized and nonparasitized nests ($U=49$, $n_1=10$, $n_2=9$, $p>0.10$). These figures indicate that 42% of parasitized nests have a cardinal egg removed, and that on average parasitized nests lose 0.43 more cardinal eggs than nonparasitized nests during the egg laying period. These losses are likely a result of female cowbird removal of host eggs.

To determine the cost to cardinal nestlings of being in parasitized nests, nestling disappearance was noted, and nestling weights in parasitized and nonparasitized nests were analyzed in 1994. First, to determine if the incidence of nestling disappearance differed between parasitized and nonparasitized

nests, those nests known to fledge young were analyzed for differences in the number of nestlings lost prior to fledging. Nests with unknown numbers of fledglings were not included, nor were nests which were found after hatching. There was no difference in the number of cardinal nestlings present at hatching ($U=80$, $n_1=14$, $n_2=11$, $p>0.20$) or at fledging ($U=80$, $n_1=14$, $n_2=11$, $p>0.20$) between parasitized and nonparasitized nests (Table 1). Similarly, no difference was found in the number of nestlings lost prior to fledging in parasitized and nonparasitized nests ($U=77$, $n_1=14$, $n_2=11$, $p>0.20$).

When nestling weights were compared, no difference was found in the weights of cowbird nestlings and cardinal nestlings occupying the same nest ($T_s=8$, $n=7$, $p>0.1$). There was also no difference in the weights of cardinal nestlings in parasitized and nonparasitized nests. However, these limited data should be considered preliminary.

Nest Success

Nests were considered successful if they produced at least one fledgling. The overall success for cardinal nests during this study was 33% (38/115). There was no difference in the number of successful nests between years (15/51 nests in 1993, 23/64 in 1994) ($G_{adj}=0.54$, $df=1$, $0.5>p>0.1$). Of those nests that were successful, two were known to produce only one cowbird each, 22 produced a total of 44 cardinals, and nine nests produced at least one cardinal and one cowbird fledgling. At the five remaining successful nests from 1993, the identities of the fledglings were unknown. For cowbirds, success was measured as the proportion of fledged young per egg laid (Mayfield 1965). A total of thirteen cowbirds (5 in 1993, 8 in 1994) fledged from 67 eggs, for an overall

success of 19%.

Nest success for parasitized and nonparasitized nests was analyzed two ways. First, the number of successful nests from the egg laying stage to the incubation, nestling, and fledging stages was compared to determine differences in success across stages. Second, the number of successful nests from the egg laying to incubation, incubation to nestling, and nestling to fledgling stages was compared to determine differences within stages.

There were no differences in nest success for either parasitized or nonparasitized nests between 1993 and 1994, and therefore data were combined. Parasitized nests were significantly more successful than nonparasitized nests from the egg laying stage to the onset of incubation (G_{adj}=7.64, df=1, 0.01>p>0.005), and from the egg laying to the nestling stage (G_{adj}=4.74, df=1, 0.05>p>0.025). The difference in success from the egg laying to the fledgling stage was nearly significant (G_{adj}=3.61, df=1, p=0.06) with success in parasitized nests being higher than in nonparasitized nests (Fig. 5). When success was analyzed within stages (egg laying to incubation, incubation to nestling, and nestling to fledgling), the only significant difference was in the egg laying stage, with more parasitized nests than nonparasitized nests surviving to the start of incubation (G_{adj}=7.64, df=1, 0.01>p>0.005) (Fig. 6).

The survival of nests was also calculated using the Mayfield analysis because not all nests were found at the same stage of the nesting cycle. The overall survival of nests in 1993 was 0.28, and in 1994, 0.21. Differences in survival were not analyzed statistically, but there was an overall trend for parasitized nests to have a higher survival than nonparasitized nests (Table 2).

During this study, a general trend for increased nest success later in the season was observed (R. Breitwisch, pers. comm.). Therefore, the breeding season was divided into two nine week periods (with 31 May as the midpoint), and nest success was analyzed to determine if there were seasonal differences between and/or within parasitized and nonparasitized nests. When all nests were considered, there was a seasonal difference in nest success, with a higher percentage of nests succeeding after 31 May (G_{adj}=8.79, df=1, 0.005>p>0.001). There was no seasonal difference in the success of parasitized nests (G_{adj}=2.60, df=1, 0.5>p>0.1), but there was a seasonal increase in the success of nonparasitized nests (G_{adj}=9.90, df=1, 0.005>p>0.001) (Fig. 7). When data were pooled into nine 10-day intervals, a strong correlation between the percent success of nonparasitized nests and the period within the breeding season was found (r_s=0.812, n=9, 0.02>p>0.01). There was no such correlation found for parasitized nests (Fig. 8).

Responses to Parasitism

Patterns of parasitism were analyzed to determine if defensive mechanisms were displayed by cardinals in response to cowbird parasitism. Abandonment of a parasitized nest was observed only twice, and egg burial was observed only once. Both cases of abandonment occurred when a cowbird egg was the first egg to be laid into a nest. There were no cases of abandonment in nonparasitized nests. In the single case of apparent egg burial, it appeared that both a cowbird egg and a cardinal egg had nesting material laid over them.

Nest Site Characteristics

Nest site characteristics were studied to determine if these variables differed between parasitized and nonparasitized nests. Nest height, height of nesting tree or shrub, and nest cover (visibility) were recorded. In 1993, data were collected in late July. Nest coverage data were taken only on those nests where vegetation growth had not altered nest site characteristics (n=13). Similarly, nest height and tree height data could be taken at only 42 nests due to nest disruption. In 1994 data were collected throughout the season within several days following the completion of a nesting attempt or the discovery of an empty nest, to avoid similar problems.

The mean height for cardinal nests in 1993 was 1.8 ± 0.7 m (range: 0.8 - 4.1 m; n=42), and in 1994 it was 1.9 ± 0.5 m (range: 0.9 - 2.8 m; n=59). No difference in cardinal nest height was found between years (U=1453, n_1=42, n_2=59, p=0.14), therefore data from the two years were combined. No difference in mean height was found between parasitized and nonparasitized nests (Table 3). Thus, nest height of cardinal nests is not important in determining whether a nest will be parasitized.

The mean height of the nesting tree or shrub in 1993 was 2.8 ± 1.6 m (range: 0.9 - 8.0 m; n=42), and in 1994 it was 3.1 ± 1.9 m (range: 1.0 - 12.0 m; n = 59). No difference in tree height was found between years (U=1463, n_1=42, n_2=59, p=0.12), therefore data were combined. No difference in nesting tree height was found between parasitized and nonparasitized nests (Table 3). Therefore, the height of the nesting tree or shrub is not important in determining whether a nest is parasitized.

In 1993 the mean coverage score was 4.08 ± 1.61 (range: 1-6; n=13), and in 1994, it was 5.15 ± 1.01 (range: 1-6; n=59). There was a difference between years, and data were analyzed by year (Fig. 9). Nest cover was found to be nearly significantly different between parasitized and nonparasitized nests in 1993 ($U=33$, $n_1=8$, $n_2=5$, $p=0.067$), with parasitized nests being less visible than nonparasitized nests. No difference was found in 1994 ($U=535.5$, $n_1=28$, $n_2=31$, $p=0.13$), however, parasitized nests tended to be more visible than nonparasitized nests.

Egg Size and Shape

The mean dimensions of cardinal eggs (n=249) found during the study were 25.1 ± 1.38 mm (range: 21.5-29.3 mm) in length and 18.4 ± 0.53 mm (range: 16.3-19.6 mm) in maximum breadth. For cowbirds (n=68), the mean dimensions were 20.8 ± 0.85 mm (range: 18.9-23.1 mm) in length and 15.9 ± 0.46 mm (range: 15.0-16.8 mm) in maximum breadth. The volume of each egg was calculated using the formula for an ellipsoid ($V = \pi LB^2/6$). However, since these eggs are not true ellipsoids (Preston 1968), a value of 0.515 was used in place of $\pi/6$ for cowbird eggs (Nolan and Thompson 1978). The index of elongation was also calculated for each egg to determine its shape (Preston 1968, 1969). Only eggs in nests of known status (as parasitized or nonparasitized) were analyzed.

Clutches of three cardinal eggs were analyzed to determine if there was a sequence effect (i.e., eggs differed in size or shape according to the order of laying), as has been found by Nol *et al.* (1984). Lack of such an effect would allow inclusion of data from clutches discovered "in progress", and allow for the

testing of clutch means rather than individual cardinal eggs. In 1993, no sequence effect was found within a clutch for either volume (X_r^2=2.57, df=2, 0.5>p>0.1) or length:breadth (X_r^2=0.93, df=2, 0.9>p>0.5). Similarly, in 1994 no sequence effect was found for volume (X_r^2=1.62, df=2, 0.5>p>0.1) or elongation (X_r^2=3.38, df=2, 0.5>p>0.1). Since no sequence effect was found, clutch means were used in comparisons between parasitized and nonparasitized clutches.

Data from 1993 and 1994 were pooled after no significant differences were found between years in the volume of cardinal eggs in nonparasitized nests, the volume of cardinal eggs in parasitized nests, or the volume of cowbird eggs. When egg volumes were compared, there was a significant difference found among the three groups (H=126.63, n_1=61, n_2=51, n_3=68, p<0.0001). Further analysis showed significant differences between cowbird eggs and both groups of cardinal eggs (vs. cardinal eggs found in parasitized nests [U=3468, n_1=68, n_2=51, p<0.0001], vs. cardinal eggs found in nonparasitized nests [U=4148, n_1=68, n_2=61, p<0.0001]) (Fig. 10). However, no difference was found between the two groups of cardinal eggs (Table 3).

The ratio of length:breadth (as a measure of elongation, or shape) was compared between years, and again no differences were found in the elongation of cardinal eggs in nonparasitized nests, cardinal eggs in parasitized nests, and cowbird eggs. A significant difference was found among the three groups of eggs (H=31.23, n_1=61, n_2=51, n_3=68, p<0.0001). When further analyzed, differences were again found between the elongation of cowbird eggs and the elongation of the two groups of cardinal eggs (vs. cardinal eggs in parasitized nests: U=2581, n_1=68, n_2=51, p<0.0001; vs. cardinal eggs in nonparasitized nests: U=3119, n_1=68, n_2=61, p<0.0001) (Fig. 11). No difference was found in

the index of elongation of the two groups of cardinal eggs (Table 3).

Relationship Between Cardinal Plumage and Frequency of Parasitism

Cardinal plumage scores and the frequency of parasitism for newly banded individuals were analyzed to determine if these were correlated. Plumage score and frequency of parasitism were known for 30 females and 31 males from the two years of study (see Appendix A). No correlation was found for either female plumage or male plumage score and percent of nests parasitized (Figs. 12 and 13). Thus, plumage coloration is not a reliable predictor of parasitism frequency.

To test if age was correlated with cardinal response to parasitism, the percentage of nests parasitized for 18 adults known to be present during both years was analyzed. No difference in percentage of nests parasitized across years was found (T_s=37, n=18, p>0.10). Thus, individual cardinals may not develop defensive responses as they age or gain experience with cowbirds.

DISCUSSION

General Patterns of Parasitism

Friedmann (1929, 1963) states that the status of the cardinal as a cowbird fosterer varies in different parts of its range, although he regards cardinals to be a regular and common cowbird host. The frequency of parasitism on a particular host is independent of host density because of the generalized nature of cowbirds (Mayfield 1965, 1977, Rothstein 1975b, Hoover and Brittingham 1993). However, regional differences in the incidence of cowbird parasitism and the importance of a given species as a cowbird host have been noted in two studies (Wiens 1963, Hoover and Brittingham 1993). This variation is likely due to differences in parasite density (McGeen 1972, Mayfield 1977), and the position of a particular species in a regional community with respect to the abundance of other hosts in that community (Wiens 1963). Therefore, to characterize the host status of cardinals in southwestern Ohio, results from this study were compared with eight other studies from different geographic locations (see Table 4).

Reported frequencies of cowbird parasitism on cardinal populations vary from 8.3 to 100% (Table 4). Population data for the listed study areas indicate that cardinal densities are highest in Illinois and Ohio, and lowest in Ontario (Robbins *et al.* 1986). When the results of the different studies were compared, no difference in the frequency of parasitism, with respect to six different

geographic locations, was found (G_{adj}=2.83, df=5, 0.9>p>0.5). There was also no correlation between the frequency of parasitism and relative cardinal density in these areas (r_s=-0.43, n=6, p>0.10). These data support the hypothesis that the frequency of parasitism is independent of host density. The parasitism frequency of 46% reported here illustrates that cardinals in southwestern Ohio are frequently parasitized and supports Friedmann's (1929, 1963) conclusion that cardinals are a frequent host to cowbirds.

As mentioned above, the frequency and intensity of cowbird parasitism on any host species is strongly dependent upon the density of cowbirds in a given area (McGeen 1972, Mayfield 1977, Hoover and Brittingham 1993). Data on the population densities of cowbirds in the listed study areas (see Table 4) indicate that cowbird populations are most dense in Kansas and Oklahoma, and least dense in Ohio (Robbins *et al.* 1986). However, no correlation between the relative cowbird density and the frequency of parasitism on cardinal nests for these studies was found (r_s=-0.6, n=6, p>0.10).

Another measure of cowbird laying activity is the intensity of parasitism. Scott (1963) defines parasitic intensity simply as the number of cowbird eggs per parasitized nest. Reported measures for parasitic intensity on cardinal populations vary from 1.0 to 2.0 eggs per parasitized nest (Table 4). There was no correlation between parasitic intensity and relative cowbird density for these studies (r_s= 0.3, n=6, p>0.10). However, when ranked, the value from this study was second lowest.

McGeen (1972) defined a second measure of parasitic intensity as the frequency of multiple cowbird eggs (the number of cowbird eggs laid in multiply parasitized nests/the total number of cowbird eggs). Reported measures for the

frequency of multiple cowbird eggs vary from 0 to 100% (Table 4). Too few data were present to test this measure of intensity. However, when ranked, the value from this study was again second lowest. These data suggest that the intensity of cowbird parasitism on this population of cardinals is lower than in other areas, possibly as a result of lower cowbird densities in southwestern Ohio. This conclusion is tentative due to both the small sample sizes of other studies and possible differences in investigator methods. While the current study focused strictly on the cardinal:cowbird relationship, other studies may reflect only casual observations on cardinal nests, producing potentially biased results. Nonetheless, the lower values of both parasitic intensity and cowbird population density for this study suggest that these may indeed be related.

Wiens (1963) noted that the frequency of parasitism on a particular host species is dependent upon the position of that species in a regional community relative to the abundance of other hosts in that area. On this study site, there are 52 species known to be parasitized by cowbirds (see Appendix B) (J. Ritzenthaler, pers. comm.). Friedmann (1963) considers 27 of these species (including cardinals) to be frequent cowbird hosts, while those remaining are rare or infrequent hosts.

It has been suggested that cardinals suffer a higher frequency and intensity of parasitism early in the breeding season, due to the sudden onset of breeding in cowbirds and the lack of other available hosts (Laskey 1950, Scott 1963). Data from Bent (1940, 1942, 1946, 1948, 1949, 1950, 1953, 1958, 1968) on the breeding seasons of other frequent cowbird hosts present on the study site, indicate that the number of host species actively breeding increases from three (including the cardinal) in mid-April, to 11 by mid-May, with all species

breeding by 1 June. It has also been suggested that female cowbirds are capable of maintaining maximal reproductive activity throughout the breeding season (Mayfield 1960, Scott 1963, Scott and Ankney 1980, 1983, Holford and Roby 1993). If both suggestions apply to this population, it would be expected that parasitism frequency and intensity would be highest early in the season due to the lack of other available hosts, and decline as the season progressed as other hosts became available.

In the current study, though there was no seasonal pattern for parasitic intensity, there was a negative correlation between the frequency of parasitism and progression of the breeding season. These data suggest that the frequency of parasitism in cardinal nests decreases throughout the season. Thus, greater incidence of parasitism in cardinal nests early in the season seems likely in this population. However, since patterns of parasitism were not determined for other host species, further data need to be collected to test this hypothesis of cowbird concentration on cardinal nests early in the breeding season.

Egg and Nestling Success

Results from this study indicate that there was no difference in the number of cardinal young fledged per parasitized and nonparasitized nest. However, data from this study also indicate that 42% of parasitized nests had cardinal eggs removed, and on average 0.43 more cardinal eggs were lost from parasitized than nonparasitized nests during egg laying. These higher losses in parasitized nests are presumably due to female cowbirds removing cardinal eggs, and are similar to other published estimates for cowbird egg removal (Hann 1941, Scott 1977, Nolan 1978, Clark and Robertson 1981, Zimmerman

1983, Burgham and Picman 1989, Scott *et al.* 1992, Sealy 1992).

In general, the primary source of host reproductive loss to parasitism is reduced nestling success due to cowbird nestlings outcompeting host nestlings. This has been shown to be especially true in smaller hosts (Friedmann 1963, Nolan 1978, Marvil and Cruz 1989, Weatherhead 1989), although it does occur in larger hosts (Rothstein 1975b). Other important factors in nestling competition are the relative growth rate and incubation period of host and parasite (Friedmann 1963, Rothstein 1975b). Cardinal nestlings in this study showed similar survival in parasitized and nonparasitized nests. There was also no apparent difference in the nestling weights of cardinals in parasitized and nonparasitized nests. These results are similar to those of Weatherhead (1989) for Red-winged Blackbirds (a host larger than cowbirds [Ricklefs 1968]), and suggest that cardinals may have life history characteristics which reduce the effects of nestling competition on cardinals in parasitized nests.

Adult cardinals are similar in size to adult cowbirds (adult cardinals weigh ca. 43 g, adult male cowbirds ca. 46 g, and adult female cowbirds ca. 39 g [Baldwin and Kendeigh 1938, Ricklefs 1968]). Cardinal eggs are significantly larger than cowbird eggs. The cardinal incubation period of 12-13 days (R. Breitwisch, pers. comm.) is similar to that of other frequent hosts and to cowbirds (Bent 1940, 1946, 1948, 1949, 1950, 1953, 1958, 1968), and data from this study indicate that no cowbird egg hatched prior to a cardinal egg.

These findings support the view that some cardinal life-history characteristics (adult body size, incubation period, and nestling growth rate) may decrease the effect of nestling competition. However, they do not discount the possibility that cardinal nestlings pay some cost for sharing the nest with a

cowbird nestling. Other studies have shown a positive correlation between the body mass or condition of nestlings at or near the time of fledging and subsequent survival (Garnett 1981, Krementz *et al.* 1989, Hochachka and Smith 1991, Magrath 1991). Cowbird nestlings in cardinal nests do surpass the weight of cardinal nestlings, thus, cowbirds may be outcompeting cardinals, thereby decreasing their overall fitness and reducing their survival. Similarly, although no mechanism has been suggested, cowbird fledglings may obtain more care from their host parents (i.e., feeding and defense) than the host juveniles, reducing their fitness, and decreasing their probability of survival. Data comparing the survival of cardinal juveniles from parasitized and nonparasitized nests may allow for a more accurate determination for the costs of being parasitized.

Nest Success

There was an overall trend in this study for parasitized nests to be more successful than nonparasitized nests. It could be argued that human disturbance at the nest resulted in fewer nests succeeding. However, attempts were made to standardize both the number and length of nest visits, therefore, differences in nest success can not be attributed to differences in human disturbance.

The increased success of parasitized nests was due to higher predation in nonparasitized nests during egg laying. It could be argued that due to the methods of data collection, nests may have been incorrectly classified as nonparasitized, producing biased results. Nest visits generally occurred at least 30 min after the daily period of egg laying (cowbirds lay prior to sunrise

[Friedmann 1929, 1963] and cardinals within an hour after sunrise [pers. obs.]). Thus, both parasitism and predation could have occurred prior to nest visitation. Similarly, if female cowbirds choose which nest to parasitize prior to laying in them, and the nest was predated prior to parasitism occurring, a nest which would have been parasitized was considered nonparasitized.

To address this argument, the time of predation in ten nonparasitized nests, and the time of 24 parasitism events was determined. From these data, the number of nests which would have been parasitized was calculated, and success in parasitized and nonparasitized nests was reanalyzed. Following analysis, the difference in nest success during egg laying between parasitized and nonparasitized nests was no longer significant (G_{adj}=3.23, df=1, 0.08>p>0.07). Similarly, the difference in overall nest success between parasitized and nonparasitized nests became insignificant (G_{adj}=0.759, df=1, 0.5>p>0.1). Thus, differences in nest success may not be as great as suggested.

A second trend observed in this study was increased nest success in the second half of the season. Seasonal increases in nest success have been demonstrated in other studies (Nolan 1963, Thompson and Nolan 1973, Gottfried and Thompson 1978). However, in this study, success in parasitized nests was higher than in nonparasitized nests before 31 May. Similarly, a significant seasonal increase in success was observed only in nonparasitized nests. The mechanism for these differences is undetermined, and requires further investigation.

This study suggests that parasitized nests are equally successful as parasitized nests. Rothstein (1975b) notes that in nearly all cases of brood

parasitism, the host suffers greater reproductive losses than nonparasitized individuals. Other studies demonstrate that for various hosts, including cardinals, success in parasitized nests is less than in nonparasitized nests (Wiens 1963, Newman 1970, Nolan 1978, Finch 1983). Only one study (Weatherhead 1989) has shown that host success in parasitized nests is equal to, or exceeds, success in nonparasitized nests. In his study, Weatherhead suggests that the result may be a product of cowbirds selecting superior nests, although, after experimental analysis, he concluded that it was a result of chance. Similar experiments were not conducted in this study, and other studies of cardinals indicate decreased success in parasitized nests. Therefore it is difficult to explain the current result, and I am inclined to conclude that this observed difference is due to chance.

It is unclear how a host would benefit from being parasitized. Smith (1968) suggested a unique mechanism for increased success in nests parasitized by the Giant Cowbird (*Scaphidura oryzivorous*), but no such mechanism has been described for hosts of the Brown-headed Cowbird. Success in parasitized nests may reflect the quality of parental care provided by the host. Adult cardinals have been shown to display only moderate aggressiveness towards models of potential predators (Nealen 1993), thus, differences in success would not be due to differences in defense. It is possible that there are differences in parental ability in feeding nestlings (Filliater and Breitwisch, unpubl. data). Nestlings present in the nests of better feeding parents would be advantaged, and cowbird young in the nest would receive the same advantage. However, data on predictors of parental ability (i.e., adult cardinal plumage phenotype) show no correlation between individual plumage

color and frequency of parasitism. Therefore, the mechanism for higher success in parasitized nests of this study is undetermined, and warrants further investigation.

Responses to Parasitism

Investigations of host defenses against cowbird parasitism have shown that in most of the species tested there was uniformity in their response, and species could be classified as either "accepters" or "rejecters" (Rothstein 1971, 1975a,b). Cardinals are considered to be an accepter species (Rothstein 1971), although they are known to abandon nests and bury eggs in response to parasitism (Bent 1968, Hill 1976, Graham 1988).

Cardinals accepted 94% of all acts of parasitism in this study. Preliminary data were also collected on female cardinal behavior at nests with and without experimentally added cowbird eggs. Data were collected on the "chip" rate (a form of cardinal vocalization which may act as a defensive or alarm call [Lemon 1968, Kinser 1973]) and the lag time until returning females sat on clutches following experimental addition of a cowbird egg. Results from this pilot study showed no difference in female behavior at manipulated and nonmanipulated nests, and indicate that cardinals showed little overall response. Egg ejection was never observed in this study. However, anecdotal evidence suggests that cardinals may be able to eject cowbird eggs from the nest. In two instances, cardinal eggs were cracked slightly while measurements were being taken, and placed back in the nest; neither egg was in the nest the following day. At another nest, two cracked eggs (one cardinal and one cowbird) were discovered in incubation; on the next visit, neither egg was present.

Further, there is little evidence for active defense against female cowbirds by cardinals in this population. Although variability in response to a model female cowbird placed at the nest was shown in the same population (Nealen 1993), these responses are likely general responses to intruders at the nest and not directed specifically at cowbirds.

It has also been shown that hosts to Brown-headed Cowbirds display a level of aggressiveness in defensive behavior proportional to the intensity with which they are parasitized (Robertson and Norman 1976, 1977). Graham (1988) observed desertion at 52% of parasitized cardinal nests in Ontario. Results from the current study suggest that cardinals in southwestern Ohio exhibit no defensive response. Since the intensity of cowbird parasitism on cardinal nests has been shown to be higher in Ontario (Scott 1963) than in Ohio, cardinals in southwestern Ohio may not be under the same level of pressure to evolve defensive responses to cowbirds.

It has been suggested that the historical duration of exposure to cowbird parasitism may predict the evolution of defensive behavior in a given host species (Rothstein 1975b). Studies have shown that Yellow Warblers (*Dendroica petechia*) in Ontario evolved defensive behavior soon after being exposed to cowbirds (less than 100 years) (Burgham and Picman 1989, Hobson and Sealy 1989). Data indicate that although cowbirds and cardinals expanded into Ohio and Ontario at about the same time (mid- 1800's) (Mayfield 1965, Bent 1968), cardinals in Ontario exhibit frequent defensive behavior (Graham 1988), while those in southwestern Ohio show no defensive behavior. These findings indicate that although cardinals in southwestern Ohio have been exposed to

cowbird parasitism long enough to evolve an effective defensive response, they are "accepters" of cowbird parasitism.

Female Cowbird Nest Selection

It has been suggested that both nest characteristics (location, structure, and size) and egg characteristics (size, shape, and color pattern) may be involved in female cowbird nest choice (King 1973, Lowther 1979, Thompson and Gottfried 1981). Data from this study indicate that in 1993, 1) parasitized nests were less visible than nonparasitized nests, and 2) cowbird eggs were less elongated than cardinal eggs in nonparasitized nests, but were not different from cardinal eggs in parasitized nests. These results were not supported by the data from 1994. In 1994, parasitized nests were more visible than nonparasitized nest, and cowbird eggs were found to be significantly less elongated than cardinal eggs in parasitized and nonparasitized nests. Thus, it would appear that nest site and nest content characteristics are not important in cowbird selection of cardinals nests.

The differences in nest cover between years may have been a result of severe weather during the winter of 1993-94. Multiflora rose (*Rosa multiflora*) is a preferred nesting site for cardinals. However, much of the multiflora rose was lost during the winter to severe cold and did not bloom the following summer. Second, an ongoing project by the staff at Aullwood involved clearing out areas of bush honeysuckle (*Diervilla lonicera*), again removing preferred nesting sites for cardinals. The loss of this vegetation may have led to higher visibility of cardinal nests.

Conclusions

Data from this study support the conclusion of Rothstein (1975b) which suggests that cardinals are a frequently used, but only moderately harmed host. Results from this study indicate that cardinals in southwestern Ohio are a frequent host to cowbirds, although the intensity of cowbird parasitism on this cardinal population is less than in other populations. Parasitized cardinals pay an egg cost of ca. 0.43 eggs per nest to cowbird removal of host eggs. However, they do not suffer nestling losses due to competition with cowbird nestlings. Thus, cardinals in southwestern Ohio are able to rear successfully their own offspring along with cowbirds. The frequency of defensive response by cardinals is less in this population than in other areas, possibly as a result of the lower intensity in cowbird parasitism. Even though cardinals in this population are as able to produce fledglings in parasitized as in nonparasitized nests, caring for the parasite may reduce the parent's chances of postbreeding survival (Rothstein 1975b). Thus, a defensive mechanism against cowbirds would presumably be better than passive acceptance.

Further investigation is necessary to determine the mechanisms for higher nest success in parasitized than nonparasitized nests. It is possible that incidence of parasitism is related to the quality of host parents. Cowbirds may choose individuals within the host population for their parenting ability. However, any mechanism for assessing this quality in potential hosts is unknown.

APPENDICES

APPENDIX A: NORTHERN CARDINAL PLUMAGE AND BILL COLOR SCORES

Method of scoring

Plumage and bill color for all Northern cardinals banded during 1993 and 1994 were scored by standard methods (which supersede those of Filliater-Lee 1992 and Nealen 1993). Plumage of the breast for males and the underside of the wing for females was scored. Bill color was scored for each bird captured. The following are the point scores assigned for the respective hue, value and chroma scores which make up each individual color rank. Point scores for each of the two body regions analyzed were summed to give a total color score for each bird. Higher total scores represent a greater intensity of red color.

Hue	Point score		Value	Point score		Chroma	Point score
6.25	4		3	4		6	1
7.5	3		4	3		8	2
8.75	2		5	2		10	3
10	1		6	1		12	4
						14	5
						16	6
						18	7

Northern cardinal color scores

A total of 31 males and 30 females were scored in 1993 and 1994. Tables A1 and A2 present the male and female plumage and bill color scores for all birds for which nesting data were also collected. Fig. A1 shows the distribution of male and female scores in the population.

Sex differences

There was a significant difference between male and female bill scores ($U=733.5$, $n_1=30$, $n_2=31$, $p=0.0001$), and male breast and female underwing score ($U=913.5$, $n_1=30$, $n_2=31$, $p<0.0001$). These differences produced an overall difference in male and female color score ($U=906$, $n_1=30$, $n_2=31$, $p<0.0001$), with males scores being higher than female scores.

Table A1. Male Northern cardinal plumage and bill color scores.

Male #	Body region	Color ranking	Score	Total score
448	Upper Breast	7.5R 4/16	12	21
	Bill	7.5R 5/12	9	
449	Upper Breast	7.5R 4/14	11	22
	Bill	7.5R 5/16	11	
450	Upper Breast	7.5R 4/16	12	21
	Bill	8.75R 5/14	9	
452	Upper breast	7.5R 4/12	10	20
	Bill	7.5R 5/14	10	
453	Upper breast	7.5R 4/14	11	21
	Bill	7.5R 5/14	10	
454	Upper breast	7.5R 4/16	12	22
	Bill	7.5R 5/14	10	
455	Upper breast	7.5R 4/16	12	22
	Bill	7.5R 5/14	10	
458	Upper breast	7.5R 5/16	11	18
	Bill	10R 5/12	7	
459	Upper breast	7.5R 4/16	12	22
	Bill	8.75R 4/14	10	
460	Upper breast	7.5R 4/14	11	19
	Bill	8.75R 5/12	8	
462	Upper breast	7.5R 4/14	11	19
	Bill	8.75R 5/12	8	
465	Upper breast	8.75R 4/14	10	18
	Bill	8.75R 5/12	8	

Table A1. (Continued).				
Male #	Body region	Color ranking	Score	Total score
466	Upper Breast	8.75R 4/14	10	19
	Bill	8.75R 5/14	9	
468	Upper Breast	7.5R 4/14	11	19
	Bill	8.75R 5/12	8	
471	Upper Breast	7.5R 4/14-16	11.5	20.5
	Bill	8.75R 5/14	9	
474	Upper Breast	7.5R 4/12-14	10.5	19
	Bill	8.75R 4-5/12	8.5	
475	Upper Breast	7.5R 4/14-16	11.5	19
	Bill	10R 5/12-14	7.5	
478	Upper Breast	7.5R 4/14-16	11.5	20.5
	Bill	8.75R 5/14	9	
487	Upper Breast	7.5R 4/14	11	21
	Bill	8.75R 4-5/14-16	10	
488	Upper Breast	7.5R 4/12	10	16.5
	Bill	10R 5/10-12	6.5	
496	Upper Breast	7.5R 4/12-14	10.5	19.5
	Bill	8.75R 5/14	9	
499	Upper Breast	7.5R 4/14	11	20
	Bill	8.75R 4/12	9	
503	Upper Breast	7.5R 4/14-16	11.5	20
	Bill	8.75R 4-5/12	8.5	
513	Upper Breast	7.5R 5/16	11	20.5
	Bill	8.75R 4-5/14	9.5	

Table A1. (Continued).				
Male #	Body region	Color ranking	Score	Total Score
515	Upper Breast	7.5R 4/14-16	11.5	20.5
	Bill	8.75R 4/12	9	
530	Upper Breast	7.5R 4/14-16	11.5	20.5
	Bill	8.75R 4/12	9	
436	Upper Breast	7.5R 4/14-16	11.5	21
	Bill	8.75R 4-5/14	9.5	

Table A2. Female Northern cardinal plumage and bill color scores.				
Female #	Body region	Color ranking	Score	Total score
039	Underwing	7.5R 5/12	9	18
	Bill	7.5R 5/12	9	
456	Underwing	8.75R 5/12	8	15
	Bill	10R 5/12	7	
457	Underwing	8.75R 5/12	8	15
	Bill	10R 5/12	7	
461	Underwing	8.75R 6/14	8	16
	Bill	8.75R 5/12	8	
463	Underwing	7.5-8.75R 5/16	10.5	17.5
	Bill	10R 5/12	7	
430	Underwing	7.5R 5/12	9	17
	Bill	8.75R 5/12	8	
412	Underwing	7.5R 5/14	10	18
	Bill	8.75 5/12	8	
467	Underwing	7.5R 5/14	10	18
	Bill	8.75R 5/12	8	
473	Underwing	8.75R 5/12	8	15.5
	Bill	10R 4-5/12	7.5	
476	Underwing	8.75R 5-6/12	7.5	15.5
	Bill	10R 5/14	8	
477	Underwing	8.75R 5/12	8	16.5
	Bill	8.75R 4-5/12	8.5	
480	Underwing	8.75R 5/12	8	16
	Bill	10R 5/14	8	

Table A2. (Continued).

Female #	Body region	Color ranking	Score	Total score
486	Underwing	8.75R 5/12-14	8.5	17.5
	Bill	8.75R 4/12	9	
489	Underwing	10R 6/12-14	6.5	14.5
	Bill	8.75R 5/12	8	
490	Underwing	8.75R 5/14	9	17
	Bill	10R 5/14	8	
494	Underwing	8.75R 5-6/12-14	9	17.5
	Bill	10R 5/14-16	8.5	
495	Underwing	10R 5/14	8	15
	Bill	10R 5/12	7	
497	Underwing	8.75R 5/14	9	16
	Bill	10R 5/12	7	
498	Underwing	8.75R 5/12	8	17
	Bill	8.75R 5/14	9	
516	Underwing	8.75R 5/12-14	8.5	15.5
	Bill	10R 5/12	7	
517	Underwing	8.75R 5/14	9	18
	Bill	10R 5/16	9	
518	Underwing	8.75R 5/12-14	8.5	16
	Bill	10R 5/12-14	7.5	
522	Underwing	8.75R 5/14	9	16.5
	Bill	10R 5/12-14	7.5	
523	Underwing	7.5-8.75R 5/12-14	9	16
	Bill	10R 5/12	7	

Table A2. (Continued).

Female #	Body region	Color ranking	Score	Total score
437	Underwing	7.5R 5/14	10	18
	Bill	8.75R 5/12	8	
456	Underwing	7.5R 5/14	10	18
	Bill	8.75R 5/12	8	
441	Underwing	8.75R 5/14	9	17
	Bill	10R 5/14	8	

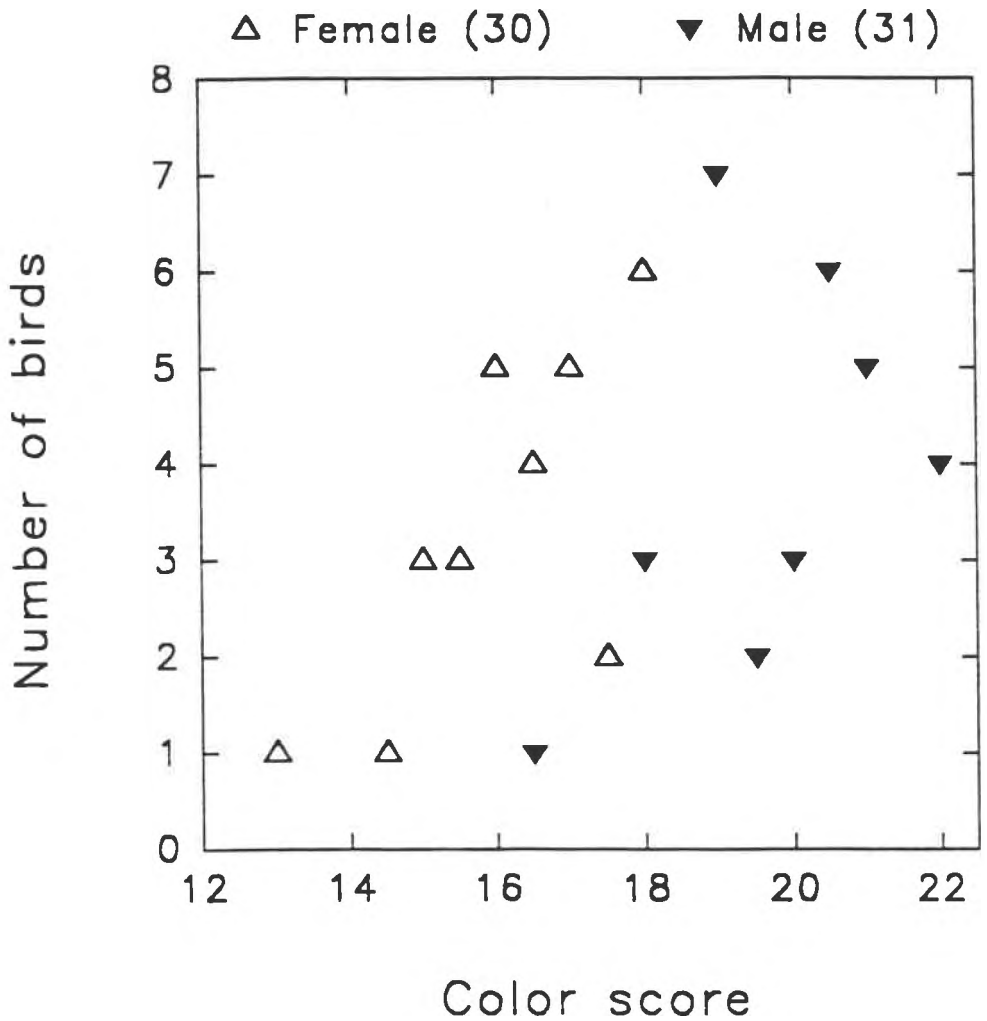

Figure A1. Distribution of male and female color scores for all scored birds (1993–1994).

APPENDIX B: THE BREEDING BIRDS OF AULLWOOD

The following is a list of known hosts to cowbirds which nest at the Aullwood Audubon Center and Farm. The common name, Latin name, and status as a cowbird host are listed.

Those birds with greater than 100 reports of cowbird parasitism[a]:

Eastern Phoebe	*Sayornis phoebe*
Yellow-throated Vireo	*Vireo flavifrons*
Red-eyed Vireo	*Vireo olivaceus*
Yellow Warbler	*Dendroica petechia*
Ovenbird	*Seiurus aurocapillus*
Common Yellowthroat	*Geothlypis trichas*
Yellow-breasted Chat	*Icteria virens*
Indigo Bunting	*Passerina cyanea*
Rufous-sided Towhee	*Pipilo erythrophthalmus*
Chipping Sparrow	*Spizella passerina*
Song Sparrow	*Melospiza melodia*
Red-winged Blackbird	*Agelaius phoeniceus*

Those birds with between 50 and 100 reports of cowbird parasitism[a]:

Eastern Wood Pewee	*Contopus virens*
Wood Thrush	*Hylocichla mustelina*
Warbling Vireo	*Vireo gilvus*
Louisiana Waterthrush	*Seiurus motacilla*
Scarlet Tanager	*Piranga olivacea*
Northern Cardinal	*Cardinalis cardinalis*
American Goldfich	*Carduelis tristis*

[a] Data from Friedmann (1963)
[b] Known rejecters of cowbird parasitism (Rothstein 1971)

Those birds with between 25 and 50 reports of cowbird parasitism[a]:

Brown Thrasher[b]	*Toxostoma rufum*
Eastern Bluebird	*Sialia sialis*
Blue-gray Gnatcatcher	*Polioptila caerulea*
Acadian Flycatcher	*Empidomax virescens*
White-eyed Vireo	*Vireo griseus*
Blue-winged Warbler	*Vermivora pinus*
White-throated Sparrow	*Zonotrichia albicollis*
Gray Catbird[b]	*Dumetella carolinensis*

Those birds with fewer than 25 reports of cowbird parasitism[a]:

Killdeer	*Charadrius vociferus*
Mourning Dove	*Zenaida macroura*
Eastern Kingbird[b]	*Tyrannus tyrannus*
Great Crested Flycatcher	*Myiarchus crinitus*
Barn Swallow	*Hirundo rustica*
Blue Jay[b]	*Cyanocitta cristata*
Carolina Chickadee	*Parus carolinensis*
Black-capped Chickadee	*Parus atricapillus*
Tufted Titmouse	*Parus bicolor*
White-breasted Nuthatch	*Sitta carolinensis*
House Wren	*Troglodytes aedon*
Carolina Wren	*Thryothorus ludovicianus*
Mockingbird	*Mimus polyglottos*
American Robin[b]	*Turdus migratorius*
Cedar Waxwing[b]	*Bombycilla cedrorum*
European Starling	*Sturnus vulgaris*
Cerulean Warbler	*Dendroica cerulea*
House Sparrow	*Passer domesticus*
Eastern Meadowlark	*Sturnella magna*
Northern Oriole	*Icterus galbula*
Common Grackle	*Quiscalus quiscula*
Grasshopper Sparrow	*Ammodramus savannarum*
Field sparrow	*Spizella pusilla*
Yellow-billed Cuckoo	*Coccyzus americanus*
Black-billed Cuckoo	*Coccyzus erythropthalmus*

[a] Data from Friedmann (1963)
[b] Known rejecters of cowbird parasitism (Rothstein 1971)

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VITA

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Thesis Title: Northern Cardinal response to brood parasitism by Brown-headed Cowbirds.

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Interests:

avian behavioral ecology
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evolutionary biology

Table 1. Number of cardinal eggs laid, number remaining at the onset of incubation, and the number of nestlings hatched and fledged in parasitized and nonparasitized nests.

Variable	Parasitized (n)	Nonparasitized (n)	U[a]	level of significance
Cardinal eggs laid	2.96 ± 0.47 (23)	2.82 ± 0.39 (17)	218.5	NS [b]
Cardinal eggs present at incubation	2.35 ± 0.65 (23)	2.65 ± 0.61 (17)	247	NS
Cardinal nestlings at hatching	2.14 ± 0.66 (14)	2.09 ± 0.70 (11)	80	NS
Cardinal nestlings at fledging	2.14 ± 0.66 (14)	2.09 ± 0.70 (11)	80	NS

[a] Man-Whitney U-tests
[b] Not significant at p=0.05

Table 2. Survival of parasitized and nonparasitized cardinal nests in 1993 and 1994.

	Overall		Parasitized		Nonparasitized	
Stage of nesting cycle	1993 (n)[a]	1994 (n)	1993 (n)	1994 (n)	1993 (n)	1994 (n)
Egg laying	0.73 (32)	0.73 (29)	0.90 (15)	0.86 (16)	0.59 (17)	0.56 (13)
Egg incubation	0.69 (40)	0.42 (48)	0.79 (22)	0.48 (26)	0.54 (18)	0.37 (22)
Nestlings	0.54 (28)	0.67 (33)	0.67 (17)	0.74 (18)	0.35 (11)	0.67 (15)
Overall	0.28 (51)	0.21 (62)	0.47 (25)	0.30 (31)	0.11 (26)	0.14 (31)

[a] n = the number of nests analyzed at each stage

Table 3. Site and content characteristics of parasitized and nonparasitized cardinal nests.

Variable	Parasitized (n)	Nonparasitized (n)	U[a]	level of significance
Nest height (m)	1.9 ± 0.6 (48)	1.8 ± 0.6 (53)	1379	NS[b]
Nesting tree height (m)	3.0 ± 1.6 (48)	3.0 ± 1.9 (53)	1355	NS
Cardinal egg volume (cm^3)	4.51 ± 0.39 (51)	4.44 ± 0.42 (61)	1726	NS
Cardinal egg shape (length/width)	1.36 ± 0.07 (51)	1.37 ± 0.08 (61)	1580	NS

[a] Mann-Whitney U-tests
[b] Not significant at p=0.05

Table 4. Studies of cowbird parasitism on populations of cardinals in different geographic locations.

Source	Location	% Nests Parasitized (n)	Cowbird eggs per parasitized nest [a]	% Multiple Cowbird eggs [b]	Cardinal relative pop. densities [c]	Cowbird
Norris (1947)	Pennsylvania	0.38 (8)	1.33	0.50	11.0	10.3
Berger (1951)	Michigan	0.45 (22)	1.90	0.84	5.7	15.5
Ely (1957)[d]	Oklahoma	0.08 (12)	2.00	1.00	17.3	29.4
Wiens (1963)[d]	Oklahoma	1.00 (4)	1.00	0.00	17.3	29.4
This study (1994)	Ohio	0.46 (122)	1.30	0.43	19.1	9.6
Scott (1963)[e]	Ontario	0.60 (187)	1.98	---	0.6	10.9
Robinson (1992)	Illinois	0.55 (20)	1.70	---	19.3	0.2
Hill (1976)	Kansas	1.00 (3)	---	---	13.5	38.2
Graham (1988)[e]	Ontario	0.28 (97)	---	---	0.6	10.9

[a] measure of cowbird parasitic intensity (Scott 1963)
[b] measure of cowbird parasitic intensity (Wiens 1963)
[c] as measured by the mean number of birds per route (Robbins *et al.*1986)
[d,e] These studies came from the same geographic location, therefore, for analyses, their results were combined

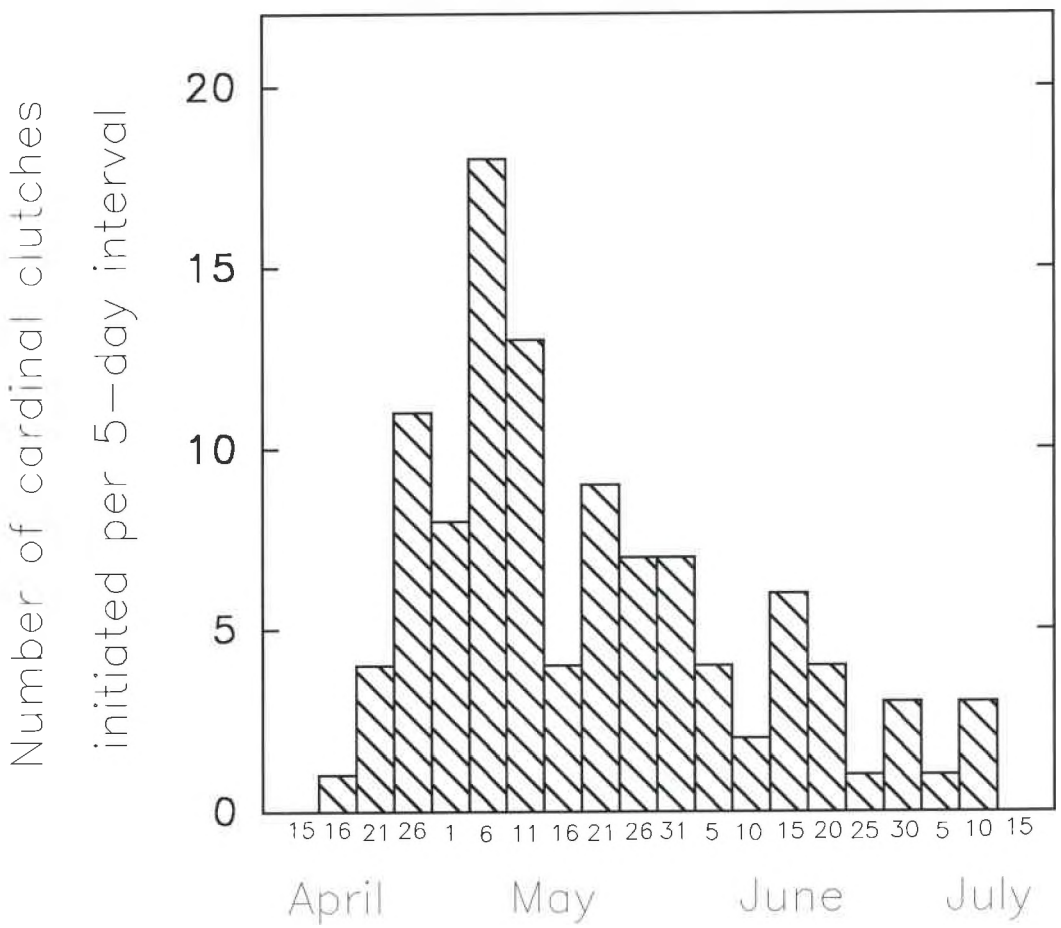

Figure 1. The distribution for the initiation of cardinal clutches during 1993–94.

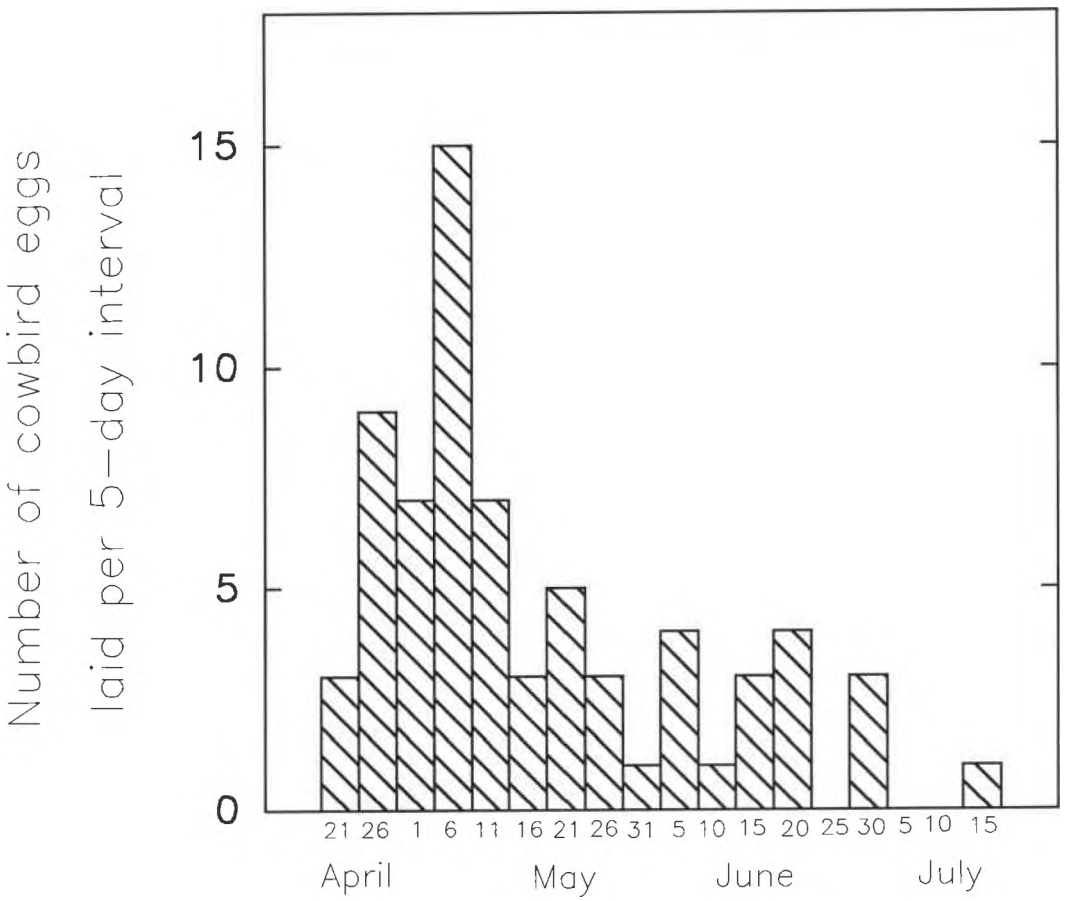

Figure 2. The distribution of cowbird eggs laid in cardinal nests during 1993–94.

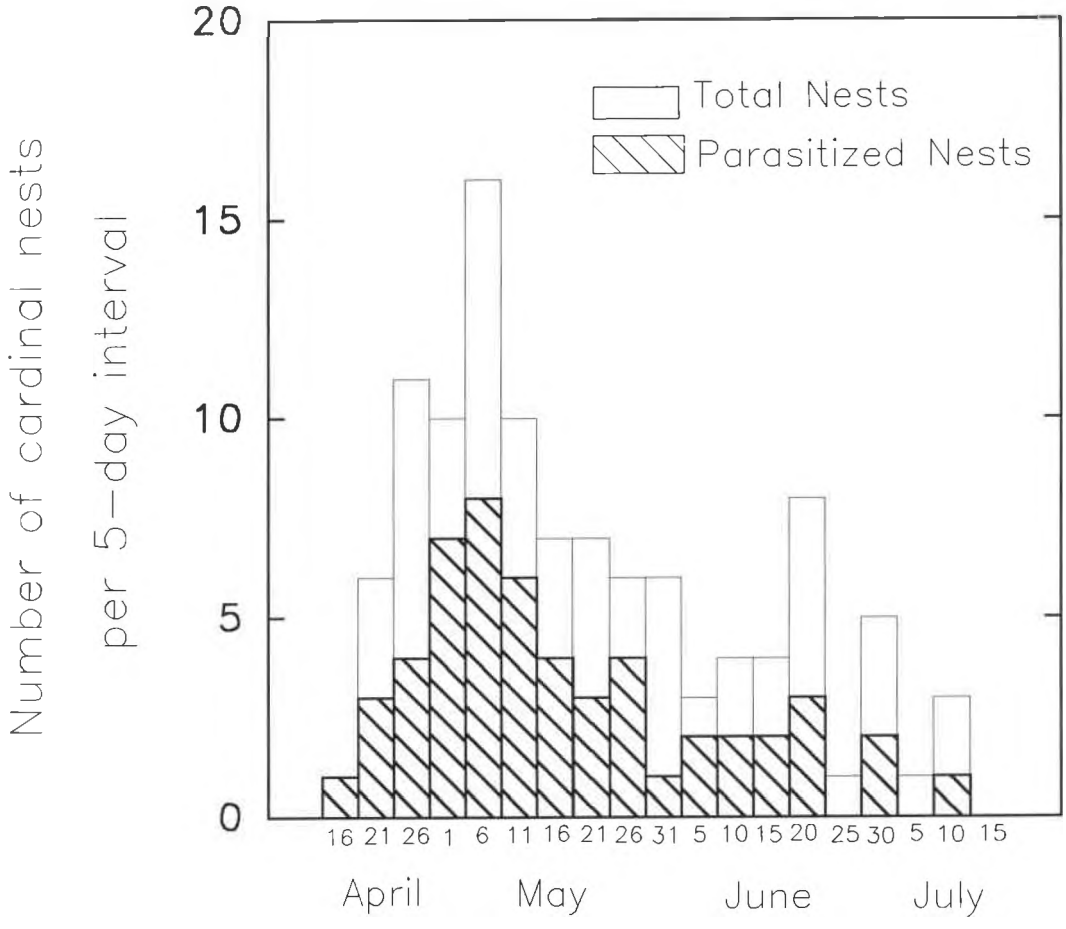

Figure 3. Frequency of cowbird brood parasitism of cardinal nests during 1993–94.

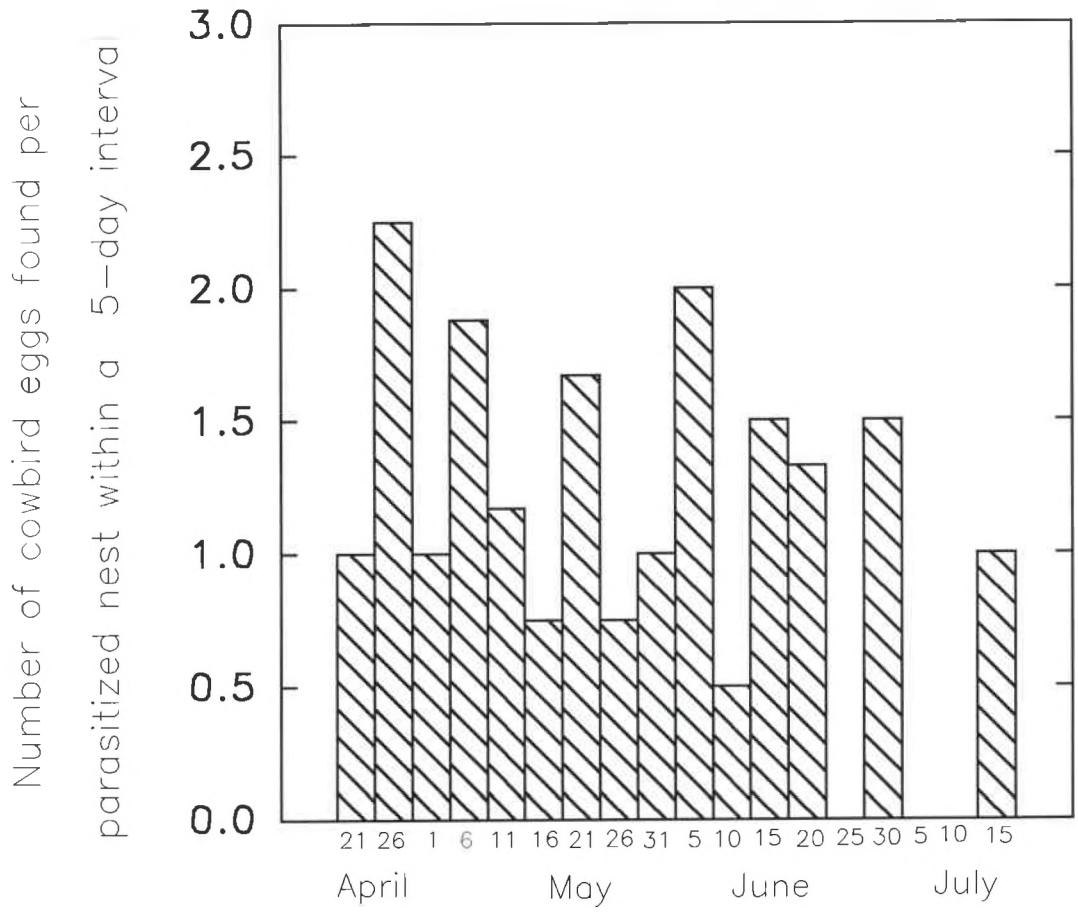

Figure 4. Seasonal variation in the intensity of cowbird parasitism on cardinal nests during 1993–94.

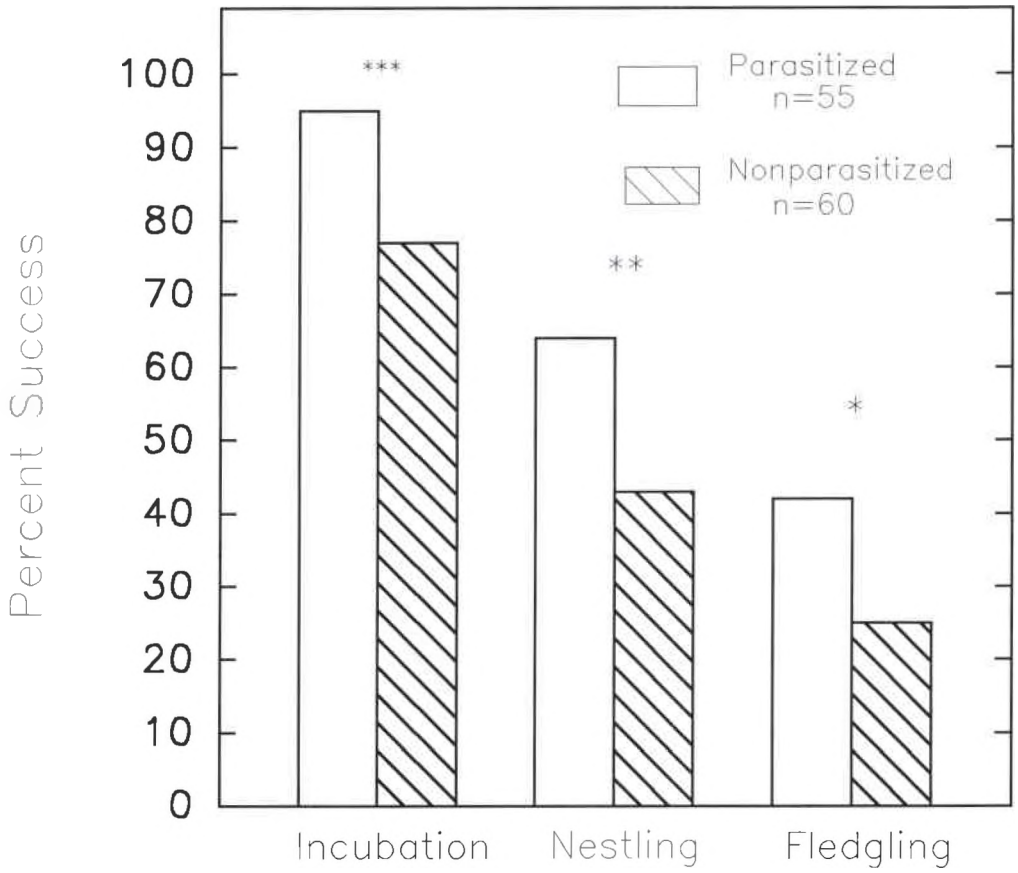

Figure 5. Cardinal nest success for parasitized and nonparasitized nests across stages (1993–1994). Differences in success from the egg laying stage to the incubation, nestling, and fledgling stages were analyzed by G-tests (* $p=0.06$; * $0.05>p>0.025$; *** $p<0.001$).

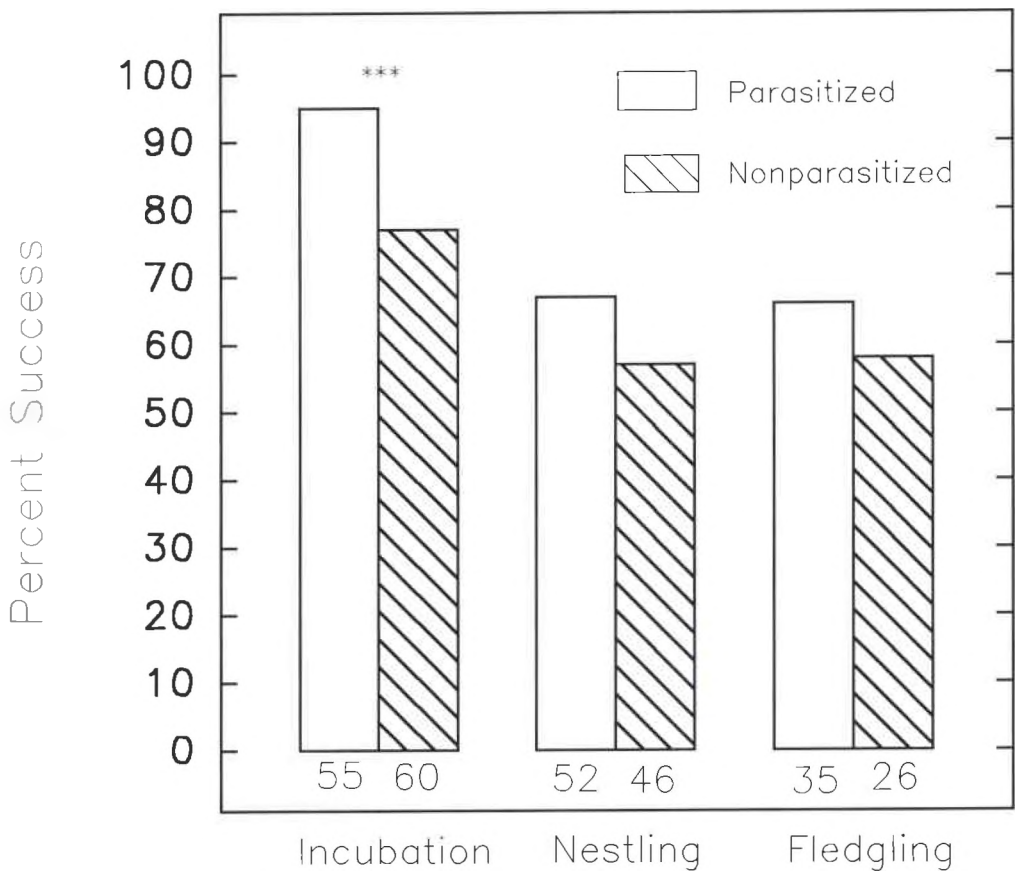

Figure 6. Cardinal nest success for parasitized and nonparasitized nests within stages (1993–1994). Differences in nest success within stages (egg laying to incubation, incubation to nestling, nestling to fledgling stages) were analyzed by G–tests (*** $0.01>p>0.005$).

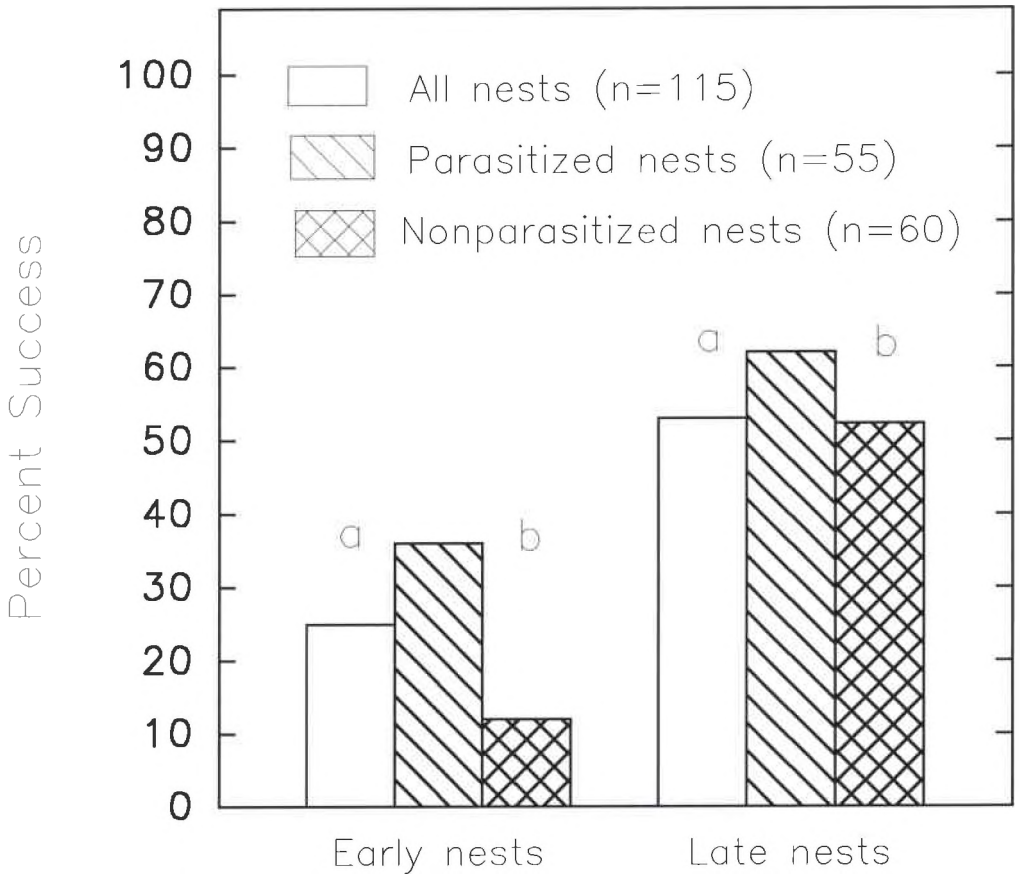

Figure 7. Seasonal increases in cardinal nest success. Percent nest success increased in all three categories of nests after 31 May, with significant increases for all nests, and nonparasitized nests (G-test: a,b $0.005>p>0.001$)

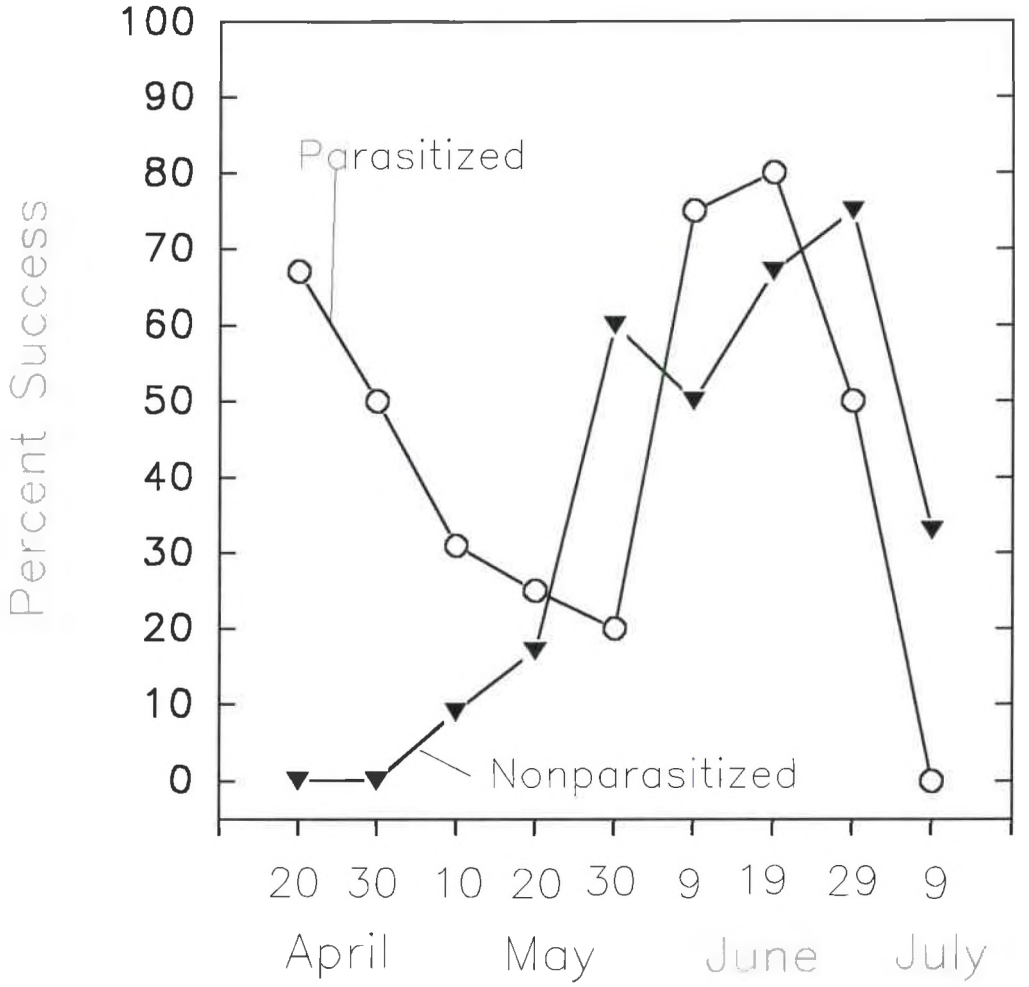

Figure 8. Seasonal trends in nest success of parasitized and nonparasitized cardinal nests.

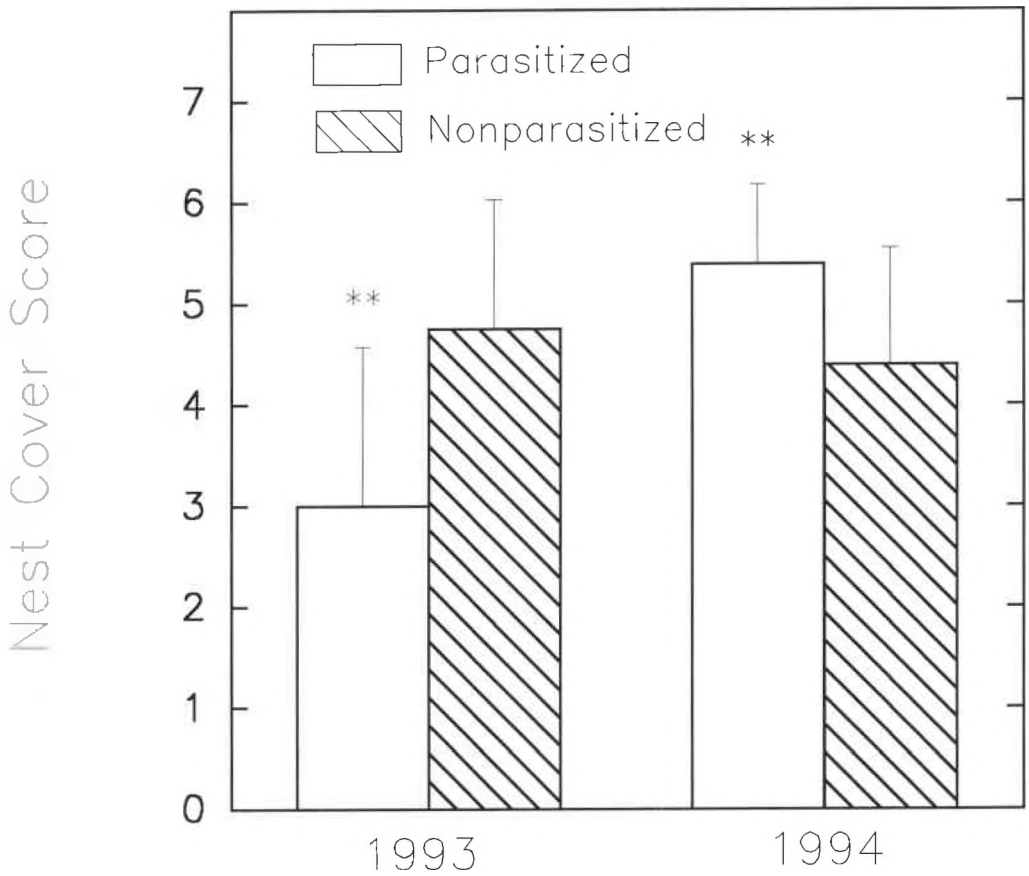

Figure 9. Nest cover of parasitized and nonparasitized cardinal nests during 1993–94 ($\bar{x} \pm$ sd).
** Mann–Whitney U test: U=129.5; p=0.003

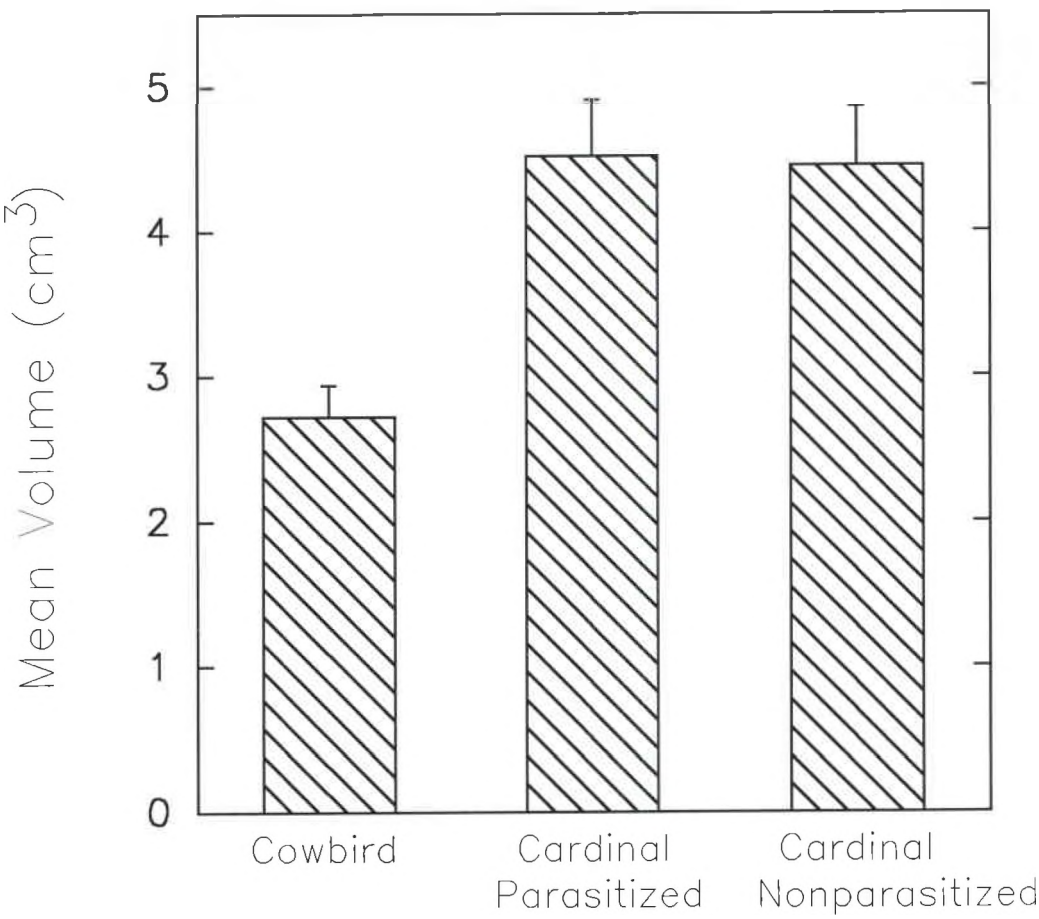

Figure 10. Volume of cardinal and cowbird eggs ($\bar{x}$ + sd). There is no difference between the two groups of cardinal eggs, but there is a difference between cowbird eggs and each of the two groups of cardinal eggs. Mann-Whitney U test: $p<0.0001$

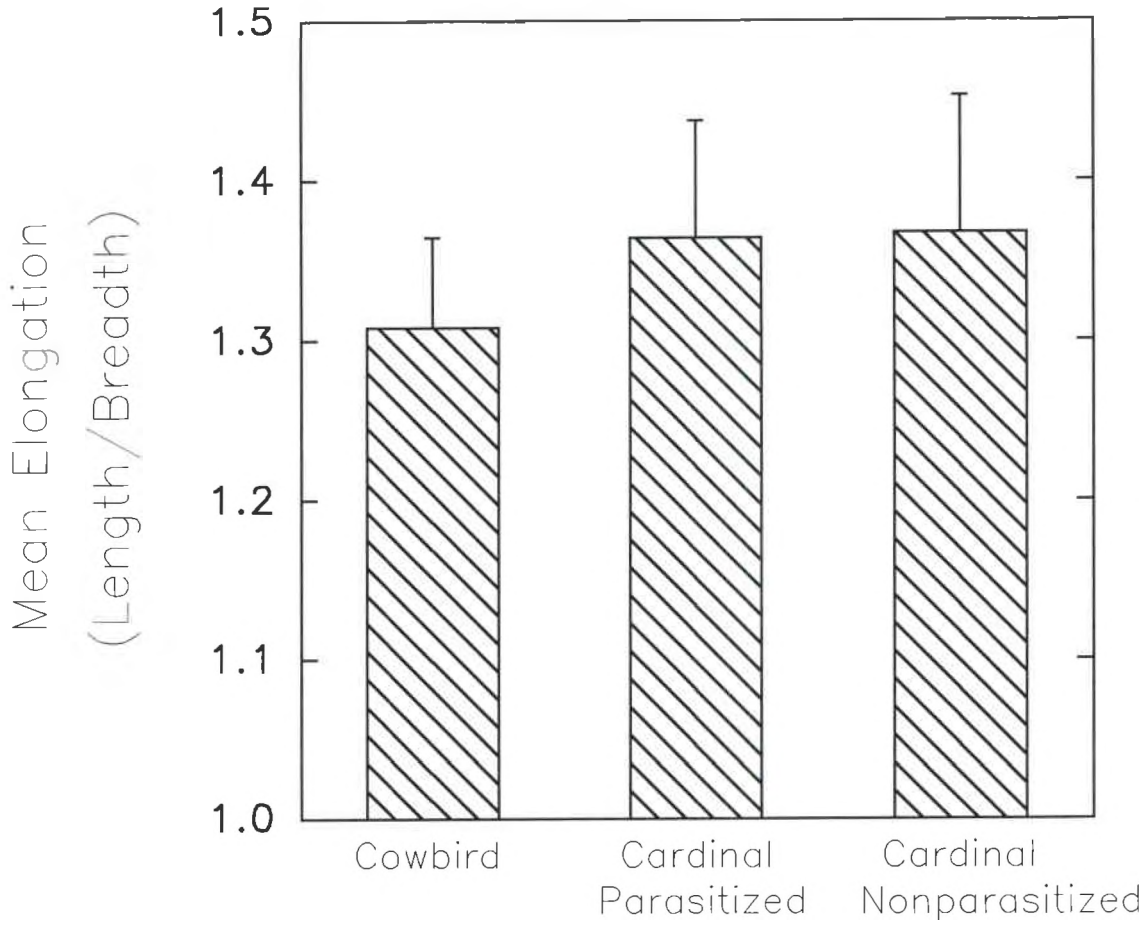

Figure 11. Elongation of cardinal and cowbird eggs ($\bar{x}$ + sd). There is no difference between the two groups of cardinal eggs, but there is a difference between cowbird eggs and each of the two groups of cardinal eggs. Mann–Whitney U test: $p<0.0001$

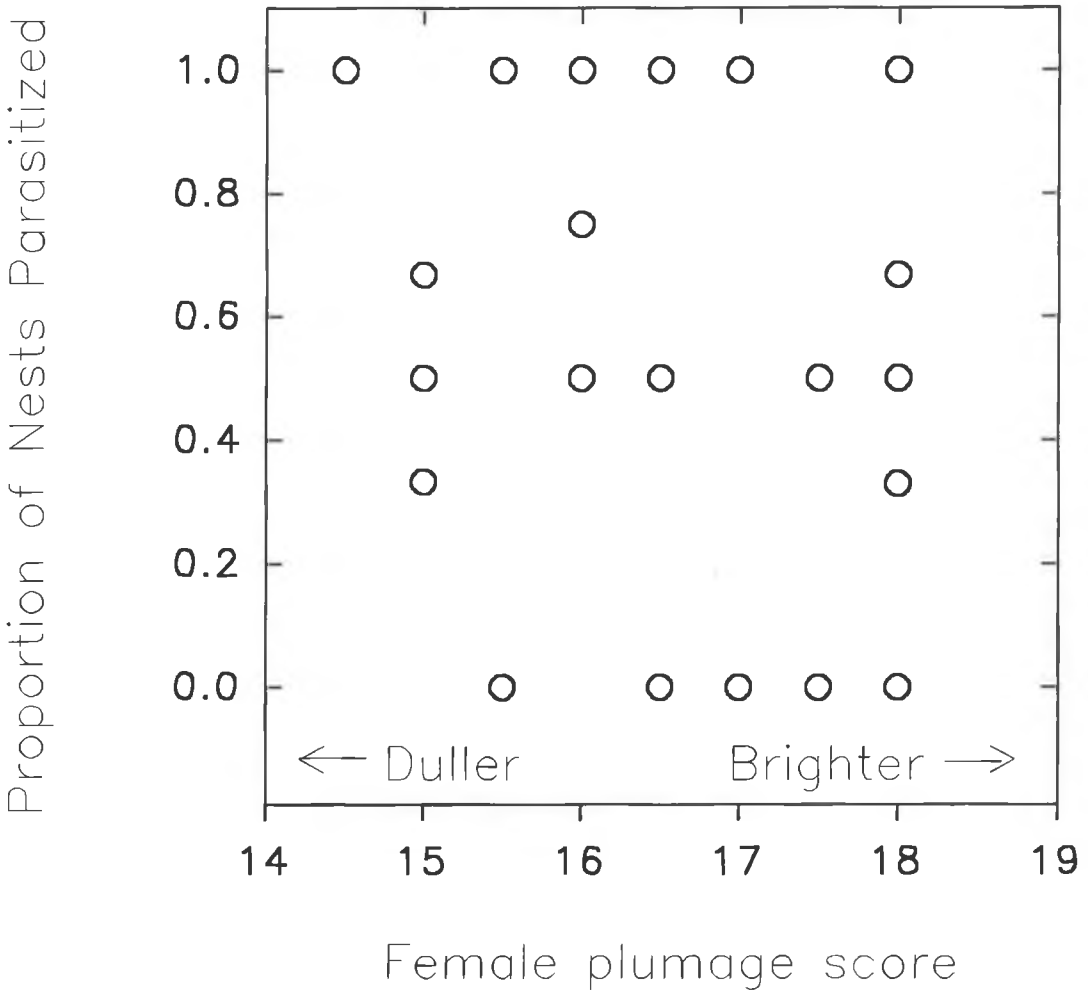

Figure 12. Relationship between female cardinal plumage score and proportion of nests parasitized ($r_s = -0.12$, $p > 0.5$).

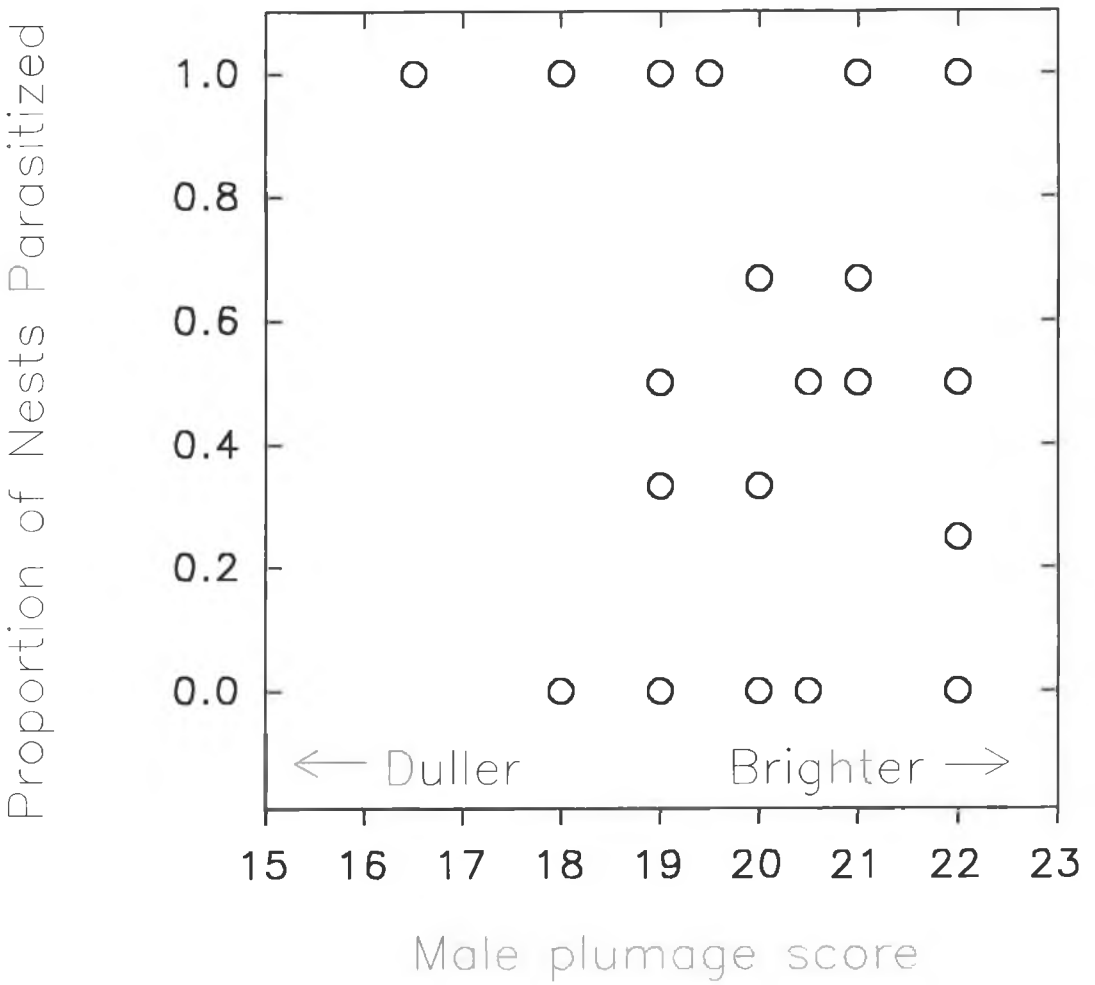

Figure 13. Relationship between male cardinal plumage score and proportion of nests parasitized ($r_s = -0.04$, $p > 0.5$).